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THE ORDOVICIAN TRILOBITE
FAUNAS OF SOUTH SHROPSHIRE, IV

W. T. DEAN

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THE ORDOVICIAN TRILOBITE FAUNAS
OF SOUTH SHROPSHIRE, IV



BY
WILLIAM THORNTON DEAN, Ph.D.

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THE ORDOVICIAN TRILOBITE FAUNAS OF SOUTH SHROPSHIRE, IV

By WILLIAM THORNTON DEAN, Ph.D.

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SYNOPSIS

The trinucleid genus *Broeggerolithus* is recorded and figured from the Actonian Stage, and the specimens assigned to *B. transiens* (Bancroft). Specimens of *Tretaspis* are figured for the first time from Shropshire and described as *T. ceriodes* (Angelin) *favus* subsp. nov. The distribution and relationships of all the known Caradoc trilobites in south Shropshire are discussed.

I. INTRODUCTION

THIS publication forms the fourth and final part of a series of bulletins covering the Ordovician (Caradoc) trilobites of south Shropshire. The first three parts contained descriptions of all the families of trilobites known in the district, and it was intended that the present paper should include subsequent discoveries, as well as summarizing our knowledge of the Caradoc trilobites in England and parts of Wales. In addition to my later collecting, the extensive material obtained during the Geological Survey's re-mapping of the Church Stretton One-inch Sheet 166 has been generously placed at my disposal, and I am indebted to Dr. F. W. Anderson and Mr. J. D. D. Smith for their co-operation. Although some new fossiliferous localities have resulted from this survey, no species has been discovered which had not previously been collected from other localities. None of the specimens has been found to necessitate a departure from the scheme of stages and zones with their associated shelly faunas propounded by the late B. B. Bancroft, whose remarkable researches received so little recognition thirty years ago. Present-day knowledge of the detailed equating of the graptolite with the trilobite/brachiopod zones still leaves much to be desired,

and the whole question of Caradoc correlation is beset with difficulties resulting from the constantly changing pattern of the boundaries of faunal provinces and facies, now known to have been far more complex than was at one time realized. Nevertheless, the basic framework of Bancroft's stages seems to afford the obvious approach to problems of Middle and Upper Ordovician correlation, and has already proved highly promising in northern England, North Wales, parts of South Wales, and areas of Shropshire to the west of the type Caradoc district. I am indebted to Professor W. F. Whittard who, as so often before, has read the manuscript and offered much useful advice.

II. SYSTEMATIC DESCRIPTIONS

Family TRINUCLEIDAE Hawle & Corda 1847

Subfamily CRYPTOLITHINAE Angelin 1854

Genus **BROEGGEROLITHUS** Lamont 1935

TYPE SPECIES. *Cryptolithus broeggeri* Bancroft by original designation of Lamont (1935 : 320).

Broeggerolithus nicholsoni (Reed)

1910. *Trinucleus nicholsoni* Reed : 212, pl. 16, figs. 1-9.

1962. *Broeggerolithus nicholsoni* (Reed) Dean : 79. Includes full synonymy.

The species was described from strata which Reed believed to be Dufton Shales near the village of Melmerby, Cumberland. The rocks, to which the name Melmerby Beds has since been applied, form part of the complex Cross Fell Inlier and are known to be of Longvillian age. Although most of the specimens from Melmerby, including practically all the original syntypes, derive from what are thought to be Lower Longvillian beds, the species ranges upwards into the early part of the Upper Longvillian, and has recently been redescribed (Dean 1962 : 79).

In an earlier paper (Dean 1959 : 120), before *B. nicholsoni* was adequately known, *Broeggerolithus simplex* was described from the Lower Longvillian Substage of the Onny Valley. More recently it has been suggested that the two species are synonymous (Dean 1962 : 81), and *B. nicholsoni* has been confirmed at the following localities in south Shropshire, all comprising rocks of Lower Longvillian age. *a.* Various exposures in Rookery Wood, east of Horderley ; *b.* the small quarry in Longville Plantation, 740 yards north-west of the Earthwork at Cheney Longville ; *c.* Long Lane Quarry, two-thirds of a mile south-west of Cheney Longville ; *d.* the large roadside quarry 280 yards south-east of Glenburrell Farm, Horderley ; *e.* the cutting just east of Chatwall Farm, four and a half miles north-east of Church Stretton, though the evidence here is somewhat fragmentary. Localities *a.*, *b.* and probably *e.* are in the zone of *Dalmanella indica* and *D. lepta* ; *c.* and *d.* are in the zone of *Dalmanella horderleyensis*.

The contemporaneous *Broeggerolithus globiceps* is undoubtedly closely related to *B. nicholsoni* and possibly represents no more than a variety. The same may also be said of *Broeggerolithus longiceps*, though the latter is stratigraphically later in south Shropshire.

Broeggerolithus transiens (Bancroft)

(Pl. 1, figs. 1-4)

1929. *Cryptolithus transiens* Bancroft : 90, pl. 2, fig. 5.1960. *Broeggerolithus transiens* (Bancroft) Dean : 123, pl. 18, figs. 2, 3, 7, 8, 11-14. Includes full synonymy of the species.

During earlier field-work in south Shropshire no reliable evidence of trinucleid trilobites was obtained from the strata of Actonian age, though one fragment of cephalic fringe, doubtfully assignable to *Broeggerolithus*, was collected from weathered Actonian sandstones at Acton Scott. More recently specimens of *Tretaspis* were found in the grey mudstone facies of the Actonian, and the collectors of the Geological Survey have recovered fragments of *Broeggerolithus* from the arenaceous facies as exposed in the old quarry 1,400 feet west-north-west of St. Margaret's Church, Acton Scott. The best-preserved of these is the internal mould of a damaged cranidium, approximately 17 mm. broad, which exhibits all the essential characteristics of *Broeggerolithus transiens*. The pit count for the four outer rows of fringe pits is estimated as follows : $E_1 + e_1 = 22$, $E_2 + e_2 = 22$, $I_1 + i_1 = 20$, $I_2 + i_2 = 21$. These figures fall within the range of variation of the species as established for specimens of Marshbrookian age (Dean 1960 : 124). The discovery of what is typically a Marshbrookian species, even though rarely, in Actonian rocks is interesting but does not affect the concept of the boundary between the Marshbrookian and Actonian Stages in south Shropshire. The base of the Actonian is well marked by the incoming of new faunal elements, and does not rely on the occasional upward extension of older species groups.

Subfamily TRETASPIDINAE Whittington 1941

Genus ***TRETASPID*** M'Coy 1849

TYPE SPECIES. *Asaphus seticornis* Hisinger by subsequent designation of Bassler (1915 : 1285).

Tretaspis ceriodes (Angelin) ***favus*** subsp. nov.

(Pl. 1, figs. 5-7 ; Pl. 2, figs. 1-6)

DIAGNOSIS. *Tretaspis* with five concentric rows of fringe pits, E_1 and I_{1-4} , developed frontally. An additional row, E_2 , developed laterally, from about R9. Approximately 22 pits in E_1 . Rows I_3 and I_4 discrete frontally but conjunct posterolaterally, at or near R18. Pygidium with five axial rings, the first four extending posterolaterally to form pleural ridges on side-lobes.

DESCRIPTION. The entire dorsal exoskeleton has not yet been found, and the subspecies is known mainly from disarticulated cranidia and rare pygidia. The cranidium is strongly convex dorsally, approximately twice as broad as long, and generally rounded in plan, though with a suggestion of angulation both frontally and anterolaterally (see Pl. 2, figs. 1, 5). The glabella is clavate in plan, with maximum breadth three-quarters of the length, and occupies about seven-eighths of the projected length of the cranidium owing to the steep declination of the

cephalic fringe frontally (see Pl. 2, fig. 5). The frontal glabellar lobe, in length about two-thirds that of the glabella, is swollen, subhemispherical, stands high above the cheek-lobes (see Pl. 2, fig. 3), and extends well in front of the latter so as to invade the area of the pitted cephalic fringe, the concentric rows of which are curved forwards medially to accommodate the glabella. The pedunculate posterior portion of the glabella is narrow, about one-third the breadth of the frontal glabellar lobe, and expands backwards to form a basal ring which is half as broad (*tr.*) as the frontal glabellar lobe. There are three pairs of glabellar furrows. Those of the first, or anterior, pair are conspicuously smaller than the others and occur only as small, almost transverse notches, indenting the sides of the glabella just behind centre. The second glabellar furrows comprise a pair of deep, reniform depressions midway between the first pair of furrows and the occipital furrow, strongly divergent forwards and placed high on the sides of the glabella at the junction of the frontal glabellar lobe and peduncle, so that they do not cut the axial furrows. The third, or basal, glabellar furrows are slightly smaller than those of the second pair, more slot-like in form, and diverge backwards strongly so as to intersect the axial furrows. As a result of the position of the glabellar furrows, what would normally be the first and second glabellar lobes are conjunct distally and merge into the proximal sides of the axial furrows. The cheek-lobes are quadrant-shaped, plump, each surmounted by a conspicuous lateral ocellus at its apex. The axial furrows are slightly divergent forwards, almost straight, deepest frontally where they contain a pair of hypostomal pits but broadening markedly towards the occipital furrow. The occipital ring is fairly large, moderately inclined backwards with maximum length at the sagittal line, separated from the glabella by a broad (*sag.*), shallow occipital furrow which deepens distally into a pair of conspicuous occipital pits, denoting a pair of apodemes.

The posterior margin of the cephalon is indented slightly at the outer ends of the occipital ring, in line with the axial furrows. In the pleurooccipital furrow a large pit is situated at each fulcrum, just inwards from the posterolateral angle of each cheek-lobe (see Pl. 1, fig. 5). These pits, although sited immediately adjacent to the innermost corners of the cephalic fringe, nevertheless appear to be distinct from that structure, and have been termed "lateral pits" by Stäuble (1953 : 91). They are considerably larger than the neighbouring fringe pits, which become progressively smaller proximally, and their function is not yet clear though the apodemes corresponding to them on the ventral surface of the test are probably concerned with the attachment of the first thoracic segment to the cephalon. They have not yet been detected in any of the other Shropshire trinucleids all of which, however, belong to a different subfamily, the Cryptolithinae. From the axial furrows as far as the fulcral pits the posterior margin of the cephalon is both transversely straight and horizontal, but then turns down and sweeps backwards to the genal angles. The latter are marked by a pair of librigenal spines of typical trinucleid form which have not yet been found completely preserved.

The greater part of the surface of the glabellar test is covered with thin, raised, anastomosing ridges which form a reticulate pattern, the superficial resemblance

of which to a honey-comb gives the subspecies its name. The reticulation is coarsest over the upper half of the frontal glabellar lobe and along the dorsal part of the "peduncle" but becomes both finer and less well defined towards the axial furrows. It dies out before reaching the axial furrows, leaving a smooth band which circumscribes the anterior margin of the frontal glabellar lobe (see Pl. 2, fig. 3) and continues backwards to the occipital furrow, at the same time encompassing the area occupied by the three pairs of glabellar furrows (see Pl. 2, fig. 6). The apex of the glabella, sited approximately at the mid-point of the frontal glabellar lobe, is topped by a small but conspicuous median ocellus. The latter scarcely protrudes above the outer surface of the test but appears larger on internal cephalic moulds. This indicates that the median ocellus involves a thinning of the test, a feature demonstrated by Størmer (1930, pl. 13, figs. 3, 5, 6) for various Norwegian species of *Tretaspis*. The reticulation immediately surrounding the median ocellus shows a suggestion of concentric arrangement proximally, but this quickly becomes obliterated distally. Likewise, there is a tendency for the reticulation to form a parallel pattern along a faint ridge developed between the median ocellus and the occiput, but both ridge and pattern quickly die out forwards.

The external surface of each cheek-lobe is covered with reticulate ridges similar to those on the glabella. The reticulation is generally coarsest on the proximal half of each cheek-lobe, but anteriorly and, more particularly, laterally it becomes finer and finally dies away, so that a smooth strip of test separates the cheek-lobe from the cephalic fringe. All the reticulation is developed only weakly on internal moulds. Each cheek-lobe carries a large, apically sited, lateral ocellus just behind centre, a position coinciding generally with the line of change from coarse to fine reticulation. There is a poorly-developed ocular ridge running forwards and adaxially from each lateral ocellus until it terminates at the axial furrow opposite the first glabellar furrows. The remainder of the cephalic test, like that of the thoracic segments and pygidium, is smooth.

The cephalic fringe is steeply declined frontally, becoming less so posterolaterally, where it is produced to form genal prolongations which extend behind the line of the pleuroccipital segment for a distance equal to a little less than one-third of the median length of the cephalon. Anteriorly the fringe is of almost uniform breadth (*exsag.*) as far as the anterolateral angles, beyond which it expands towards the genal angles. The holotype, the best-preserved specimen, shows five continuous rows of fringe-pits frontally, namely E_1 and I_{1-4} . The outermost three rows of these are transversely straight at this point, but the two innermost rows are flexed forwards a little so as to accommodate the frontal glabellar lobe. The pits of E_1 and I_1 are located close together in radial sulci at first, but beyond a point marked by R_9 or R_{10} (the exact position on the holotype is not clear owing to imperfect preservation) the sulci increase in length (*exsag.*) owing to the development of a further outer row of pits, E_2 , accompanied by a slight outward flexing of the cephalic margin. The large sulci, each containing three pits, continue as far as about R_{14} (exact position not quite clear) but then the two outermost rows continue, in smaller sulci, towards the genal angles whilst the inner row I , curves more strongly backwards to the

posterior margin, the triangular area between it and the outer two rows being occupied by an irregular complex of about eleven pits. The pit count for the holotype cranidium is as follows : $E_1=22$; $E_2=11$; $I_1=20$; $I_2=19$; I_3 and $I_4=20$, with four large pits common to both rows. Well-defined, thin, concentric ridges, or lists as they were termed by Størmer (1930 : 12), occur between I_1 and I_2 , and between I_2 and I_3 . A less conspicuous ridge exists between I_3 and I_4 as far as R_9 , beyond which it diminishes and the two rows coalesce to form a single row of large pits beyond R_{17} , there being room for three or four such pits before the margin is attained. There are eight or nine pits along the posterior margin. The ventral surface of the cephalic fringe is inadequately known, but is apparently of the type found in other species of *Tretaspis*, with a strongly developed girder, ornamented with raised terrace-lines, which extends on to the librigenal spines.

The thorax is not known.

The best-preserved pygidium, almost 9 mm. broad, is transversely semielliptical in plan, about four times as broad as long. The anterior margin, excluding the small articulating half-ring, is straight, ending in bluntly-pointed anterolateral angles. The posterior margin is uniformly curved, defined by a slightly raised marginal rim marking the upper limit of the steeply declined posterior border, which is ornamented by closely-grouped terrace-lines. The poorly differentiated axis is slightly raised above the side-lobes, from which it is separated by scarcely discernible axial furrows ; it occupies between one-third and one-quarter of the frontal breadth of the pygidium and narrows backwards only slightly. There are five axial rings, reducing in size from front to rear and separated from each other by ring furrows which become less impressed posteriorly, so that the fifth ring is separated from the marginal rim by only a faint groove. The first four axial rings are continued posterolaterally across the side-lobes as straight, raised ridges which just fail to attain the marginal rim. The ridges are smaller from first to fourth and progressively become directed more strongly backwards.

HORIZON AND LOCALITIES. The first known specimens of the new subspecies came from a small exposure in the north bank of the River Onny, about 30 yards east of its junction with the stream leading south from Batch Gutter. At this point in the succession fairly well-preserved *Tretaspis ceriodes favus* was found occurring in a band of fossil fragments within grey mudstones containing a fauna of Actonian age, including *Calyptaulax*, *Chasmops*, *Remopleurides*, *Dolerorthis* and *Onniella*. The horizon is, in fact, topmost Actonian as the fossil band was seen to be overlain by rubbly mudstones containing *Onnia? cobboldi* (Bancroft), the index fossil of the lowest zone of the Onnian Stage. These higher mudstones also yielded a few examples of *Tretaspis ceriodes favus*, suggesting that the latter has a somewhat extended vertical range, but as all are fragmentary it is also possible that they have been derived from the underlying Actonian strata. No other post-Actonian specimens are known.

The subspecies has also been found in grey mudstones of Actonian age in the neighbourhood of Cardington, three miles east-north-east of Church Stretton.

The locality is in the west bank of the stream, 20 yards south of the Corn Mill, a quarter of a mile south-east of Cardington.

HOLOTYPE. B.M. In.54718 (Pl. 1, fig. 5 ; Pl. 2, figs. 1, 3-6).

PARATYPES. B.M. In.54719 (Pl. 2, fig. 2) ; In.54721 ; In.54722 ; In.54759 ; In.55656 ; In.55662.

DISCUSSION. The new subspecies is one of a group of forms of *Tretaspis* centred on *T. ceriodes* (Angelin) and all occurring in the southern Norwegian Stage 4bδ or its equivalent, including the Actonian and Onnian Stages of the Anglo-Welsh area.

The neotype cranium of *T. ceriodes* (Størmer 1930, pl. 9, figs. 1a-d) is roughly two-thirds the size of the holotype of *T. ceriodes favus*, though with a similar number of pits in E_1 , and there is no development of E_2 . However, the upper lamella of a larger, damaged specimen figured by Størmer (1945, pl. 4, fig. 16) shows a few, perhaps four or five, large pits near the genal angle, suggesting a possible small development there of E_2 . Again in the case of the neotype, I_3 and I_4 converge at about R_{12} , that is to say farther forwards than in the Shropshire form. In the holotype of *T. ceriodes angelini* Størmer (1930, pl. 9, figs. 5a-c) the corresponding rows converge at about R_8 , and E_2 is developed from R_{10} , or perhaps R_9 . The pygidium of *Tretaspis ceriodes favus* is similar to that of *T. ceriodes* but has five axial rings, one more than the small pygidium described by Størmer (1930 : 47, pl. 9, fig. 4). However, the pygidium of a larger specimen figured later by Størmer (1945, pl. 4, fig. 16) also possesses five axial rings.

Tretaspis ceriodes donsi Størmer (1945 : 405, pl. 1, fig. 8) was founded on a single, incomplete external mould of a small cranium. On this specimen I_3 and I_4 converge at R_7 or R_8 , and there appear to be six rows of pits in front of the glabella as stated by Størmer, indicating the presence there of E_2 , though the state of preservation is not wholly satisfactory.

III. RELATIONSHIPS OF THE SOUTH SHROPSHIRE TRILOBITES

Trilobites are not known from the earliest Costonian strata in south Shropshire, but higher in the same stage their remains become progressively more abundant and in the topmost Costonian the trinucleid *Costonia* is of stratigraphical value. Although *Costonia* is a local genus, represented in south Shropshire by only two geographically separated species, it undoubtedly constitutes a development from the Anglo-Welsh genus *Marrolithus*, essentially a Llandeilo form but appearing as early as the Llanvirn Series and persisting in the Shelve Inlier as late as the Harnagian Stage (Spy Wood Grit). The Homalonotidae are well represented by the genera *Brongniartella* and *Platycoryphe* in the northern outcrops of the Costonian, though they are unknown in the south. Their derivation is problematical, but forms generally similar to *Brongniartella* have been described, as *Platycoryphe vulcani* (Murchison), from the Llanvirn Series of west Shropshire (Whittard 1961 : 164), whilst *Platycoryphe dentata* Dean (1961 : 340) may be related to the Bohemian *P. bohémica* (Barrande). Calymenid trilobites are, with few exceptions, almost ubiquitous throughout the type Caradoc succession. They make their appearance

in the higher Costonian beds but, as in the case of the trinucleids, there is some geographical differentiation in species between the northern and southern outcrops, and *Flexicalymene* (*Reacalymene*) *pusulosa* (Shirley) is found only in the north ; this is the sole recorded occurrence of *Reacalymene* from this horizon, but the subgenus has been found as far afield as Baffin Island, in rocks of somewhat uncertain age (Whittington 1954). *Flexicalymene acantha* Bancroft, in the southern outcrops around Coston, is another trilobite suggesting a derivation from a Llandeilo species-group, and shows affinities with the earlier *F. cambrensis* Salter sp. (Dean 1962a). Of the other Costonian trilobites, *Proetidella* and an occasional asaphid, *Parabasilicus powisi* (Murchison), represent families which became more abundant in the succeeding Harnagian and Soudleyan Stages, but *Metopolichas*? sp., known from only two specimens, is a rare form of Llandeilo and Baltic affinities. These are the only lichids known in south Shropshire prior to the Actonian Stage, when members of the family became more abundant, though represented by a different genus, namely *Platylchas*.

In many respects the shelly fauna of the lowest Harnagian Stage is one of the most interesting in south Shropshire. Trinucleid trilobites are generally abundant in the earlier strata and, although *Reuscholithus* and *Smeathenia* are local genera, unknown elsewhere, *Broeggerolithus harnagensis* (Bancroft) and *Salterolithus praecursor* Dean represent the earliest known members of stratigraphically important genera, the origin of which is not clearly understood, and they may represent immigrant forms. *Broeggerolithus harnagensis* is close to a species found in the Derfel Limestone of the Bala district, associated with a fauna which has been shown to have strong Baltic affinities (Whittington & Williams 1955). In south Shropshire, although some of the early Harnagian brachiopods are of Baltic type, the only trilobite which could be described thus is *Acanthoparypha stubblefieldi* (Bancroft), but the genus is known also from the Middle Ordovician of North America. The genera *Kloucekia* and *Primaspis* indicate affinities with Bohemian faunas, and the former genus subsequently became a common constituent of Longvillian faunas in England and Wales.

In recent years Choubert and others (1956 : 394) have erected the name *Sokhretia* as a subgenus of *Kloucekia*, with type species *Dalmanites solitaria* Barrande 1852, for certain Ordovician trilobites from Morocco. As has been pointed out (Dean 1961 : 327) *D. solitaria* closely resembles the Anglo-Welsh species of *Kloucekia* (*Phacopidina*), of which subgenus *Sokhretia* is here regarded as a subjective synonym. The record is interesting, however, in extending the known geographical range of *Kloucekia*. The relatively sudden appearance of the so-called "exotic" trilobite elements may be correlated with what has been termed the "*Nemagraptus gracilis* Transgression", widespread over much of England and Wales, ranging upwards in time, into the succeeding *Diplograptus multidentis* Zone (Dean & Dineley 1961), and linking faunal regions which had previously been distinct from one another. On the other hand, certain trilobite groups in the Harnagian of south Shropshire represent a continuation of families which had already become established during the late Costonian ; they include the Asaphidae (*Parabasilicus*), Homalonotidae

(*Platycoryphe*) and Proetidae (*Proetidella*). The distribution of some of the Harnagian trilobites presents as yet unsolved problems, and *Parabasilicus* is known elsewhere only in South Korea and, perhaps, South America (Kobayashi 1935 : 475 ; Harrington & Leanza 1959 : 146), whilst the only extra-British record of *Salterolithus* is from Venezuela (Whittard 1959 : 89 ; Dean 1960 : 138). Of the Calymenidae, *Flexicalymene acantha* Bancroft continues from the Costonian, whereas *Gravicalymene praecox* (Bancroft) is of uncertain origin, appearing briefly in the basal Harnagian and then apparently leaving the district until Actonian times when closely similar forms re-entered south Shropshire, again a migration which may be connected with an important marine transgression, this time late in the *Dicranograpthus clingani* Zone.

The remaining Harnagian trilobites in south Shropshire are poorly known and comprise only the trinucleids *Salterolithus caractaci* (Murchison) and *Broeggerolithus ulrichi* (Bancroft). The former belongs to a common Anglo-Welsh genus, but *B. ulrichi* is geographically restricted and has yet to be found outside the Welshpool district and, perhaps, the Onny Valley, though its existence at the latter place is doubtful.

In the Soudleyan and Lower Longvillian the general picture of the trilobite faunas is one of stability and uniformity, not only in south Shropshire but also over much of North Wales and northern England. Of the Trinucleidae, *Broeggerolithus broeggeri* (Bancroft) and *B. soudleyensis* (Bancroft) are well represented in both the Caradoc and Shelve districts and several North Welsh faunas, whilst in the Lower Longvillian, although *B. globiceps* (Bancroft) is apparently confined to Shropshire, the accompanying *B. nicholsoni* (Reed) becomes more abundant elsewhere, particularly in the argillaceous and mudstone environment of northern England (Melmerby Beds of the Cross Fell Inlier ; Drygill Shales near Carrock Fell) and the Pwllheli district of North Wales, and is of some stratigraphical value. With the exception of the uncommon and poorly-known "*Brongniartella*" *rudis* (M'Coy), a species in need of redescription (Dean 1961 : 355), the Homalonotidae are represented throughout south Shropshire and Wales by small species, such as *Brongniartella minor* (Salter), which form part of an indigenous group present in the Costonian. The same may also be said of the Asaphidae, represented by *Parabasilicus*?, and the Calymenidae, with *Flexicalymene planimarginata* (Reed), *F. (Reacalymene)* cf. *limba* (Shirley) and *F. (R.) horderleyensis* Dean. After apparently leaving the Anglo-Welsh area during the later Harnagian and the whole of the Soudleyan, *Kloucekia* returned in the Lower Longvillian, though as a different species, *K. apiculata* (M'Coy), and remained until late in the Upper Longvillian. The distribution of the pterygometopid genus *Chasmops* during the Lower Longvillian is interesting. Although members of the genus are not uncommon in North Wales, and occur also in the Melmerby district of the Cross Fell Inlier (Dean 1962 : 104), they have not been found in south Shropshire, though another species, *C. extensa* (Boeck), is abundant there later in the succession. The Illaenidae are almost unrepresented in the Anglo-Welsh area at this horizon, apart from a single record of *Stenopareia*? sp. at Cross Fell (Dean 1962 : 120).

The base of the Upper Longvillian Substage in south Shropshire is marked, at

some points of the outcrop, by a small disconformity, followed in turn by a minor marine transgression which may, perhaps, explain certain curious features of the trilobite faunas. *Brongniartella bisulcata* (M'Coy), a relatively large species of the genus, appears in some abundance at the base of the Upper Longvillian, whilst higher in the same substage the Norwegian zonal index *Chasmops extensa* makes its début. That the incoming of such forms may be of more than local significance is suggested by the occurrence in North Wales of the Baltic genus *Estoniops* (*E. alifrons* M'Coy sp.), which also reached the Cross Fell Inlier (Dean 1962 : 100) though it has not been found in Shropshire. Certain of the other Upper Longvillian trilobites in south Shropshire showed little change from those of the Lower Longvillian. The trinucleid *Broeggerolithus longiceps* (Bancroft) was very close to *B. nicholsoni* (Reed), whilst *Kloucekia apiculata* persisted unchanged. *Atractopyge* in the higher beds of the Snowdon Volcanic Series of North Wales, and *Platylchas* in the Upper Melmerby Beds of the Cross Fell Inlier, are genera unknown from this horizon in Shropshire but represent groups which occurred both earlier, in the Derfel Limestone of Merionethshire, and later, in the Actonian, Onnian and Pusgillian Stages of Shropshire and Cross Fell.

The Marshbrookian trilobite fauna of south Shropshire is of generally conservative aspect, comprising in the main genera already present in the Upper Longvillian. *Brongniartella bisulcata* and *Chasmops extensa* are both abundant and of large individual size, whilst *Broeggerolithus transiens* (Bancroft) is of stratigraphical value and represents a development from the immediately preceding *B. nicholsoni* and *B. longiceps*. *Brongniartella bisulcata* and *Broeggerolithus* cf. *transiens* are known from the same horizon in the Cross Fell Inlier (Dean 1962 : 108, 82), though not from the Welsh area, perhaps the result of non-deposition of the relevant strata rather than actual absence of the species, but there is as yet no satisfactory explanation for the absence of *Chasmops extensa* from the Marshbrookian of Cross Fell, as the species is found in a variety of environments in Shropshire. Of the Calymenidae, only *Flexicalymene caractaci* (Salter) is of consequence in Shropshire. Though possibly deriving from earlier Anglo-Welsh species, *F. caractaci* bears perhaps the strongest resemblance to the Bohemian form *F. declinata* (Hawle & Corda), but as the latter is probably of Ashgill age (Dean 1962a : 220) it may have resulted from an emigration of the British species-group, which is unknown in Shropshire after the Marshbrookian. Although *Dindymene* was recorded by Bancroft (1949, text-fig. 39) from the Actonian of the Onny Valley in south Shropshire, his claim has not been substantiated, and the only Anglo-Welsh occurrences of the genus in the Caradoc Series are in the Upper Longvillian of North Wales and the Upper Longvillian and Marshbrookian of the Cross Fell Inlier (Dean 1962 : 89), though the genus was more common in Scottish, Bohemian and Polish faunas of Caradoc and Ashgill age (Kielan 1959). *Encrinurus* has a somewhat similar distribution in Shropshire and at Cross Fell. *Otarion* and *Proetidella*? have been found only rarely, and again represent old-established families in the Anglo-Welsh area, whilst an occasional *Primaspis* in the Shropshire Marshbrookian foreshadowed the relative abundance of the genus in the succeeding Actonian.

The Actonian and Onnian Stages may conveniently be considered together here as their trilobite faunas not only have certain elements in common, but also mark a profound change from those of preceding stages. Although the stratal succession in south Shropshire is continuous from the Marshbrookian to the Onnian, over much of the Anglo-Welsh area rocks of Marshbrookian, and even Longvillian, age are absent, the result of either erosion or non-deposition. At this point in the succession there then occurs the group of dark mudstones and shales known sometimes as the Nod Glas, which is widespread over large areas of North Wales. It marks a marine transgression late in the *Dicranograptus clingani* Zone, though occasionally extending upwards into the *Pleurograptus linearis* Zone; by opening up new routes of communication with other faunal regions it must be considered largely responsible for the relatively sudden appearance of immigrant trilobite groups in the Shropshire Actonian. The family Trinucleidae, so important earlier in the succession, is only scantily represented by rare *Broeggerolithus transiens* (Bancroft) in the arenaceous facies of the middle Actonian, and by occasional *Tretaspis ceriodes favus* subsp. nov. (see p. 5) in the grey mudstones of the upper Actonian, the latter subspecies possibly extending upwards into the basal Onnian, at which point it overlaps with members of the genus *Onnia*, which become abundant and of zonal value. Of the Shropshire species of *Onnia*, *O. gracilis* (Bancroft) is somewhat difficult to place with reference to the other forms, exhibiting as it does affinities with the Bohemian *Onnia ornata* (Sternberg), and it may be that such a relationship could result from faunal migrations connected with the transgression of the Nod Glas. More conspicuous faunal links which may be correlated with the transgression are those with corresponding Scandinavian faunas. The Raphiophoridae are known for the first time in south Shropshire, with *Ampyxella edgelli* (Reed), a species virtually identical with *A. aculeata* (Angelin) from the Upper Chasmops Limestone, Etage 4bδ, of southern Norway, and *Lonchodomas pennatus* (La Touche) similarly exhibiting strong Scandinavian affinities. The calymenid genus *Onnicalymene* (Dean 1962; 1962a) appears in Shropshire in the Actonian, and ranges upwards through the Onnian in some abundance, comprising three species, *O. laticeps* (Bancroft), *O. salteri* (Bancroft) and *O. onniensis* (Shirley). The last-named occurs also in the Onnian of the Welshpool district and the Cross Fell Inlier, but in the latter district it ranges upwards through the black mudstones of the Pusgillian Stage. In both Norway and Sweden the genus is represented at the corresponding horizons, belonging to Etage 4bδ, by *Onnicalymene jemtlandica* (Thorslund). In Shropshire *Onnicalymene* replaces *Flexicalymene* sensu stricto as an important constituent of the fauna, but the relationship of the two genera is still not clear, and they may not represent a simple evolutionary series. The effects of the Nod Glas transgression may also be held responsible for the return of *Gravicalymene* in the Shropshire Actonian and, more rarely, Onnian after a long absence from the district, during which time there is as yet no evidence of its whereabouts. Of the Pterygometopidae, *Chasmops extensa* continued throughout the Actonian of Shropshire in even greater abundance than before, but disappeared early in the Onnian, whilst *Calyptaulax*, essentially an Actonian genus, is unknown later than the basal Onnian, where it is

rare. The distribution of these two genera is unusual in that *Chasmops* is rare in the Cross Fell Inlier, known from only a few fragments in the Actonian and one in the Pusgillian (Dean 1962 : 104), whilst *Calyptaulax* appears uncommonly in the Onnian of the Dufton district, becoming increasingly abundant in the Pusgillian and eventually forming an important constituent of Ashgill shelly faunas in the Anglo-Welsh area. Similarly, *Dalmanitina*, best known from the Ashgill, has not been found in Shropshire but appeared at Cross Fell in the Pusgillian, though the genus has been described from part of the *Dicranograptus* Shales (?high Caradoc in age) of South Wales (Reed 1904). As stated earlier in this paper, the encrinurid genus *Atractopyge* is found in Welsh, Scottish and North American faunas of earlier age, but it makes only a brief appearance in the Shropshire Actonian. At Cross Fell, however, *Atractopyge* appears in the Onnian and, like *Calyptaulax*, increases in numbers in the Pusgillian. A somewhat similar distribution holds for *Platylichas laxatus* (M'Coy), abundant in the Actonian of Shropshire and almost identical with forms found in the Upper Chasmops Limestone, 4bδ, of southern Norway. The Illaenidae are not generally well represented in the Anglo-Welsh Caradoc Series, and their often fragmentary remains are not well documented, but most specimens have been found in the Actonian and Onnian of Shropshire where, again, the affinities appear to lie with Scandinavian species, for example *Illaenus fallax* Holm. The Swedish olenid *Triarthrus linnarssoni* Thorslund is represented in Shropshire (Dean 1962a : 241), one of a group of related Middle Ordovician species which is widely distributed through Scandinavia and North America but has not yet been proved in the Cross Fell district. The Odontopleuridae and Otariionidae occur infrequently in the Anglo-Welsh area, apart from the Actonian of south Shropshire. *Primaspis caractaci* (Salter) is moderately common in the arenaceous facies there and exhibits affinities with slightly earlier Bohemian and eastern North American species, so that it probably represents an immigrant group, though the genus has been found rarely in the Harnagian of Shropshire and the Longvillian of Cross Fell. In spite of the fact that remopleuridid remains have been recorded from practically all the Stages of the Caradoc in the Cross Fell Inlier, this family appears in Shropshire for the first time in the Actonian, where species of *Remopleurides* are close to contemporaneous Scandinavian forms, whilst in the Shropshire Onnian only *Remopleurella* is known, a genus found elsewhere in the Upper Chasmops Limestone of Norway (Dean 1962a : 250). At Cross Fell *Remopleurella* is unknown, but *Remopleurides* increased in numbers in the higher Pusgillian and eventually, like so many other trilobite groups, assumed even greater importance in the faunas of the Anglo-Welsh Ashgill Series. The thysanopeltid *Eobronteus?* sp., and the cheirurid *Pseudosphaerexochus* sp. represent rare elements in Anglo-Welsh Caradoc faunas, and their derivation is not clear.

IV. LIST OF THE KNOWN SOUTH SHROPSHIRE SPECIES

COSTONIAN STAGE

Brongniartella caradociana Dean 1961

Costonia elegans Dean 1960

Costonia ultima (Bancroft 1949)

- Flexicalymene acantha* Bancroft 1949
Flexicalymene (Reacalymene) pusulosa (Shirley 1936)
Metopolichas? sp.
Parabasilicus powisi (Murchison 1839)
Platycoryphe dentata Dean 1961
Proetidella fearnsidesi Bancroft 1949

HARNAGIAN STAGE

- Acanthoparypha stubblefieldi* (Bancroft 1949)
Broeggerolithus harnagensis (Bancroft 1929)
Broeggerolithus ulrichi (Bancroft 1949)
Broeggerolithus? sp.
Flexicalymene acantha Bancroft 1949
Gravicalymene praecox (Bancroft 1949)
Kloucekia (Phacopidina) harnagensis (Bancroft 1949)
Parabasilicus powisi (Murchison 1839)
Platycoryphe dentata Dean 1961
Primaspis harnagensis (Bancroft 1949)
Proetidella fearnsidesi Bancroft 1949
Reuscholithus reuschi Bancroft 1929
Salterolithus caractaci (Murchison 1839)
Salterolithus praecursor Dean 1960
Smeathenia smeathenensis (Bancroft 1949)

Soudleyan Stage

- Broeggerolithus broeggeri* (Bancroft 1929)
Broeggerolithus soudleyensis (Bancroft 1929)
Brongniartella minor (Salter 1852)
Brongniartella minor subcarinata Dean 1961
Flexicalymene (Reacalymene) cf. limba (Shirley 1936)
Parabasilicus powisi (Murchison 1839)
Proetidella cf. fearnsidesi Bancroft 1949

Longvillian Stage

Lower Longvillian Substage

- Broeggerolithus globiceps* (Bancroft)
Broeggerolithus nicholsoni (Reed 1910) [= *B. simplex* Dean 1960]
Brongniartella minor (Salter 1852)
Brongniartella sp.
Flexicalymene planimarginata (Reed 1906)
Flexicalymene (Reacalymene) horderleyensis Dean 1962
Kloucekia (Phacopidina) apiculata (M'Coy 1851)
Parabasilicus? sp.
Platycoryphe? sp.

UPPER LONGVILLIAN SUBSTAGE

Asaphid indet.

Broeggerolithus longiceps (Bancroft 1929)

Brongniartella bisulcata (M'Coy 1851)

Brongniartella edgelli (Salter 1865)—horizon of this species is uncertain

Chasmops extensa (Boeck 1837)

Flexicalymene cobboldi Dean 1962

Kloucekia (*Phacopidina*) *apiculata* (M'Coy 1851)

MARSHBROOKIAN STAGE

Broeggerolithus transiens (Bancroft 1929)

Brongniartella bisulcata (M'Coy 1851)

Chasmops extensa (Boeck 1837)

Encrinurus sp. (? nov.)

Flexicalymene caractaci (Salter 1865)

Flexicalymene cobboldi Dean 1962

Otarion sp.

Primaspis caractaci (Salter 1857)

Proetidella? sp.

ACTONIAN STAGE

Ampyxella edgelli (Reed 1910)

Atractopyge sp.

Broeggerolithus cf. *transiens* (Bancroft 1929)

Brongniartella bisulcata (M'Coy 1851)?

Calyptaulax actonensis Dean 1961

Chasmops extensa (Boeck 1837)

Chasmops salopiensis Dean 1961

Gravicalymene cf. *praecox* (Bancroft 1949)

Iliaenus sp.

Lonchodomas pennatus (La Touche 1884)

Onnicalymene laticeps (Bancroft 1949)

Onnicalymene salteri (Bancroft 1949)

Otarion sp.

Platylichas laxatus (M'Coy 1846)

Primaspis caractaci (Salter 1857)

Remopleurides latus Olin *onniensis* Dean 1962

Remopleurides warburgae Dean 1962

Tretaspis ceriodes (Angelin) *favus* subsp. nov.

ONNIAN STAGE

Ampyxella edgelli (Reed 1910)

Calyptaulax actonensis Dean 1961

Chasmops extensa (Boeck 1837)

Eobronteus? sp.

Gravicalymene inflata Dean 1962

Gravicalymene cf. *praecox* (Bancroft 1949)
Illaenus cf. *fallax* Holm 1882
Lonchodomas pennatus (La Touche 1884)
Onnia? *cobboldi* (Bancroft 1929)
Onnia gracilis (Bancroft 1929)
Onnia superba (Bancroft 1929)
Onnia aff. *superba* (Bancroft 1929)
Onnicalymene onniensis (Shirley 1936)
Platylichas laxatus (M'Coy 1846)
Pseudosphaerexochus sp.
Remopleurella burmeisteri (Bancroft 1949)
Tretaspis ceriodes (Angelin) *favus* subsp. nov.
Triarthrus cf. *linnarssoni* Thorslund 1940

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EXPLANATION OF PLATES

Numbers with the prefix B.M. In. refer to material in the British Museum (Natural History) ; the remainder are in the Geological Survey & Museum (G.S.M). The specimens were whitened with ammonium chloride before photographing. Photographs by the writer.

PLATE I

Broeggerolithus transiens (Bancroft)

p. 5

Actonian Stage, old quarry 1,400 feet west-north-west
of St. Margaret's Church, Acton Scott.

FIGS. 1, 3, 4. Front, plan, and lateral oblique views of damaged cranidium preserved as internal mould. G.S.M. JD.3044. $\times 4$.

FIG. 2. Fragmentary internal mould of cephalic fringe showing girder, with pits of E_{1-2} sited in shallow, radial sulci. G.S.M. JD.3040. $\times 6$.

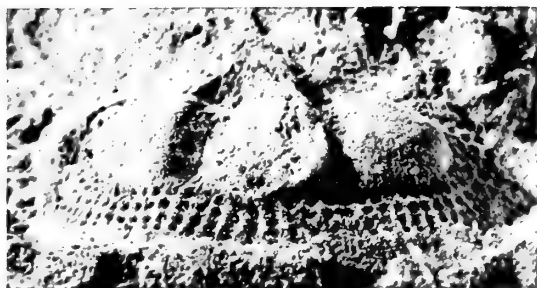
Tretaspis ceriodes (Angelin) *favus* subsp. nov.

p. 5

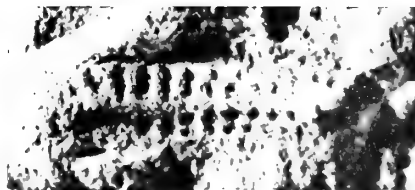
Topmost Actonian Stage, north bank of River Onny, about
30 yards east of junction with Batch Gutter.

FIG. 5. Enlarged view of left cheek-lobe showing lateral ocellus and variation in reticulation of test. B.M. In.54718. $\times 12$.

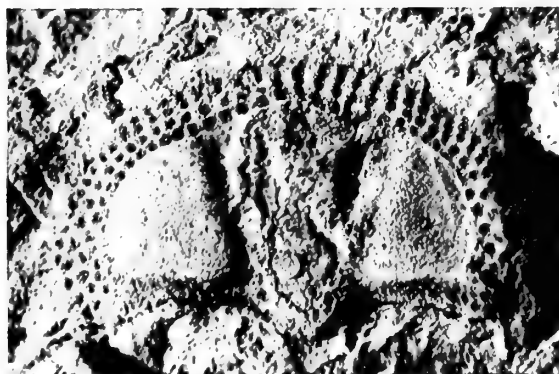
FIGS. 6, 7. Fragmentary cephalon showing radial sulci of the cephalic fringe, together with the marginal suture. B.M. In.54722. $\times 5$.



1



2



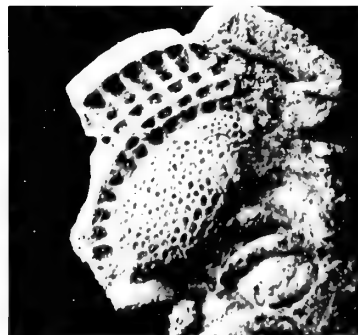
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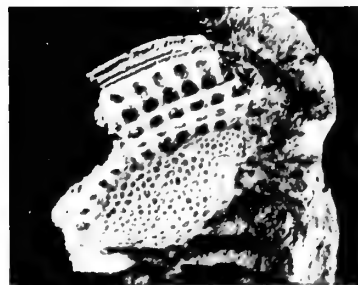
4



5



6



7

PLATE 2

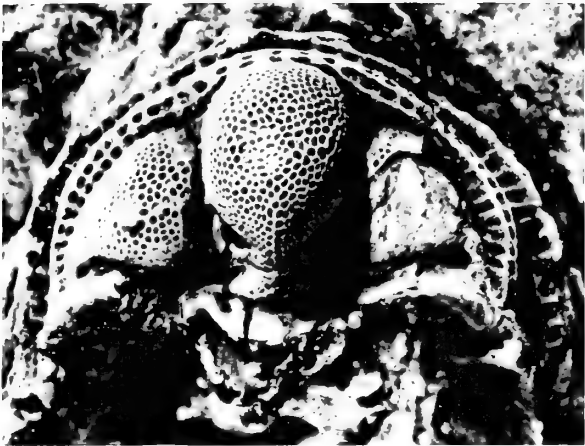
Tretaspis ceriodes (Angelin) *favus* subsp. nov. p. 5

Topmost Actonian Stage, north bank of River Onny, about
30 yards east of junction with Batch Gutter.

FIGS. 1, 3, 5. Plan, frontal and lateral views of cranium with most of test preserved.
B.M. In.54718. × 5.

FIGS. 4, 6. Enlarged views of same specimen, showing median ocellus and glabellar furrows.
× 12.

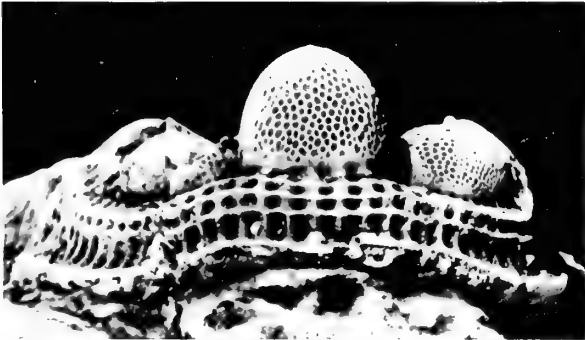
FIG. 2. Pygidium with test preserved. B.M. In.54719. × 6.



1



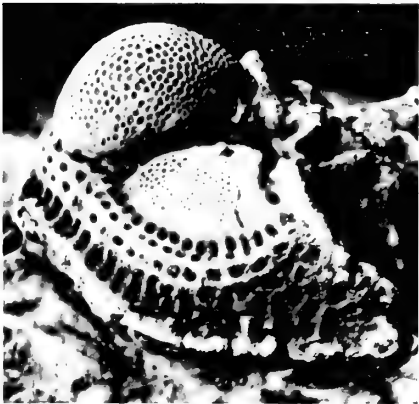
2



3



4



5



6

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MIDDLE JURASSIC OSTRACODA FROM SOUTH YORKSHIRE

R. H. BATE

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GEOLOGY

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BY
RAYMOND HOLMES BATE, Ph.D.

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SYNOPSIS

The Bajocian ostracods from the Hydraulic Limestone and associated marine sediments of South Yorkshire are described. Twenty-one genera and twenty-seven species are recorded, of which four genera and twelve species are new. Eight families within the single order Podocopida Müller 1894 are recognized. The Hydraulic Limestone/Elter Beck Bed horizon is correlated with the Kirton Cementstone Series of Lincolnshire and is considered to be of *discites* age.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

THE present paper, dealing with the marine ostracods of the Hydraulic Limestone and associated marine sediments of South Yorkshire is the second of four papers dealing with the Middle Jurassic ostracod faunas of north-eastern England.

The localities from which the samples were obtained occur both to the north and to the south of the town of Market Weighton, the latter having given its name to the stable area (in Middle Jurassic times) on which it is situated. To the north of this stable area the Middle Jurassic sediments are deltaic with occasional marine incursions, the Hydraulic Limestone representing the first such marine incursion of the Yorkshire delta, table I.

TABLE I

Generalized table of strata occurring to the north and south of Market Weighton.

<i>Strata north of Market Weighton</i>	<i>Strata south of Market Weighton</i>	<i>Stages</i>
CORNBRAsh (UPPER)	UPPER	CALLOVIAN
UPPER DELTAIC SERIES	" ESTUARINE " SERIES	BATHONIAN
GREY LIMESTONE SERIES		BAJOCIAN
MIDDLE DELTAIC SERIES (UPPER)		
MILLEPORE SERIES	CAVE OOLITE	
MIDDLE DELTAIC SERIES (LOWER)	BASEMENT BEDS	
ELLER BECK BED/ HYDRAULIC LIMESTONE	HYDRAULIC LIMESTONE	
LOWER DELTAIC SERIES	LOWER " ESTUARINE " SERIES	
DOGGER		
LIAS	LIAS	TOARCIAN

To the south of the Market Weighton "structure" the sequence is poorly exposed, the beds associated with the Hydraulic Limestone being separated from the Upper Lias by a thin sequence of Lower "Estuarine" Series. The most fossiliferous section occurs at South Cave, Eastfield Quarry (map reference SE/913323), where the ferruginous marls and rubbly limestones (Basement Beds of Neale 1958), which overlie the Hydraulic Limestone, were excavated in a working to test the thickness of the overlying Cave Oolite. This section is no longer exposed. It was, however, measured and sampled by Professor P. C. Sylvester-Bradley in 1947. Samples of marl brought up out of the working as well as the samples collected by Sylvester-Bradley were examined. The Hydraulic Limestone was sampled by the Ellerker Beck (map reference SE/927297) where it originally outcropped but is now represented only as large boulders at the surface. North of Market Weighton the most important section occurs on the Firby road near Kirkham Priory (map reference SE/738658). Here the Hydraulic Limestone is somewhat impersistent and underlain by 8 ft. of grey shale and ferruginous sandstone. Further north there are no exposures except for a disused working near Castle Howard station (map reference SE/735666). Elsewhere the course of the limestone is marked by the presence of fragments of the rock at the surface, of which a sample was collected near Ganthorpe (map reference SE/704698). Material collected from the Kirton Cementstone Series, Greetwell Quarry, Lincoln (map reference TF/002725), and not included in Bate 1963, is described in the present paper.

The change northwards of the Hydraulic Limestone, and of the marine beds associated with it, into a thick bed of ripple marked sandstone (maximum thickness 22 ft. 7 in.) with fossiliferous ironstone bands indicates the nearness of the delta front in the northern part of the Yorkshire basin. Unfortunately the lithology of the sandstone (Eller Beck Bed) is such that if any ostracods were originally present, they have long since been leached away. No ostracods have been found in the ironstone bands. Correlation of this bed with the Hydraulic Limestone is, therefore, purely stratigraphic.

The Hydraulic Limestone (maximum thickness 4 ft.) and associated marine sediments probably never total more than 18 ft. and are often considerably less. Absence of complete exposures makes an estimate of the total thickness difficult. The Hydraulic Limestone/Eller Beck Bed represents a marine transgression from the south and is to be correlated with the Lincolnshire Limestone. The similarity of the ostracod fauna (in the absence of any ammonite evidence in Yorkshire) suggests that this horizon can be fairly accurately correlated with the Kirton Cementstone Series and thus would be of *discites* age.

The work embodied in this paper was commenced in the Geology Department of the University of Sheffield. I would like to record my sincere thanks to Professor L. R. Moore for the use of the facilities of that Department. I am also deeply indebted to Professor P. C. Sylvester-Bradley for guidance throughout the research and also for the use of the departmental facilities whilst at Leicester University. The award of a D.S.I.R. research studentship grant is also gratefully acknowledged.

All registered specimens mentioned in the text are now in the Department of Palaeontology, British Museum (Natural History).

II. SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille 1806

Order PODOCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family CYTHERELLIDAE Sars 1866

Genus **CYTHERELLOIDEA** Alexander 1929

TYPE SPECIES. *Cytherella williamsoniana* Jones.

Cytherelloidea eastfieldensis sp. nov.

(Pl. 1, figs. 1-5, Text-fig. 1)

DIAGNOSIS. A *Cytherelloidea* with carapace elongate, incurved middorsally and midventrally. A prominent ridge extends around the valve periphery, bending into the centre middorsally to produce a question mark-shaped ridge. Shell surface weakly reticulate.

HOLOTYPE. Io. 900, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 901-05, horizon and locality as above.

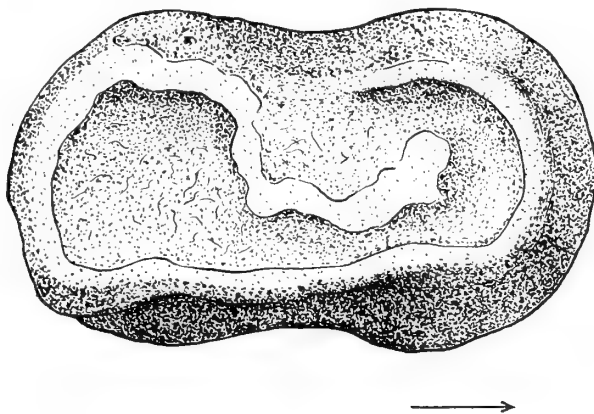


FIG. 1. Camera lucida drawing, right valve, *Cytherelloidea eastfieldensis* sp. nov., paratype Io. 901, $\times 110$ approx.

DESCRIPTION. *Carapace* subrectangular in lateral view. Dorsal and ventral margins strongly incurved medially. A prominent ridge extends around the valves, continuous except in the middorsal region where the ridge bends down into the centre of the valve to curve forwards, producing a large, question mark-shaped ridge. Depending upon the individual specimens, this ornament may be either complete or only partially developed, in which case the central ridge is separate from the peripheral ridge. Shell surface may be weakly reticulate, but dependent upon

the state of preservation. *Right valve* larger than the left which it overlaps strongly on all sides. Greatest length passes through midpoint; greatest height in the anterior or posterior third. Greatest width in the posterior third. Internally, the *muscle scars*, typical of the genus, are situated on a node just dorsal of midpoint. A shallow groove extends around the valve margin in the right valve for the reception of the left.

Dimensions

Holotype. Io. 900 carapace (Pl. 1, figs. 2-5) length 0.63 mm.; height 0.36 mm.; width 0.16 mm.

Paratypes. Io. 901 R.V. (Pl. 1, fig. 1, Text-fig. 1) length 0.68 mm.; height 0.40 mm. Io. 902 L.V. length 0.59 mm.; height 0.44 mm.

REMARKS. This species resembles *Cytherelloidea paraweberi* (Oertli 1957, pl. 1, figs. 12-15) except for the fact that the peripheral ridge in the latter is continuous around the carapace and not discontinuous middorsally as in the former.

C. eastfieldensis is not restricted to the type locality, being found throughout the Kirton Cementstone Series, Greetwell Quarry, Lincoln, where it is, however, only poorly preserved. This is not a common species.

Suborder PODOCOPINA Sars 1866

Superfamily CYPRIDACEA Baird 1845

Family PARACYPRIDIDAE Sars 1923

Genus **PARACYPRIS** Sars 1866

TYPE SPECIES. *Paracypris polita* Sars.

Paracypris bajociana Bate

1963 *Paracypris bajociana* Bate : 186, pl. 2, figs. 1-8.

REMARKS. Most common in the marl underlying the Cave Oolite (Basement Beds), South Cave, from which horizon three paratypes were selected in the original description. The species also occurs in the Hydraulic Limestone of Ellerker and in the underlying marine sediments exposed on the Firby road.

Superfamily CYTHERACEA Baird 1850

Family BYTHOCYTHERIDAE Sars 1926

Genus **MONOCERATINA** Roth 1928

TYPE SPECIES. *Monoceratina ventrale* Roth.

Monoceratina vulsa (Jones & Sherborn)

(Pl. 1, fig. 6)

1888 *Cytheridea vulsa* Jones & Sherborn : 263, pl. 2, fig. 4a-b.

1938 *Monoceratina vulsa* (Jones & Sherborn) Triebel & Bartenstein : 516, pl. 3, figs. 17, 18.

?1955 *Bythocythere aliena* Ljubimova : 34, pl. 2, fig. 3a-b.

1960 *Monoceratina* cf. *vulsa* (Jones & Sherborn) ; Lutze : 433, pl. 37, fig. 5a-b.

1963 *Monoceratina vulsa* (Jones & Sherborn) ; Bate : 189, pl. 3, figs. 5-12.

REMARKS. This is not a common ostracod in the sediments associated with the Hydraulic Limestone and only a few isolated valves have been found in the Basement Beds (marl facies), South Cave.

Family PROGONOCYTHERIDAE Sylvester-Bradley 1948

Subfamily PROGONOCYTHERINAE Sylvester-Bradley 1948

Genus **PROGONOCYTHERE** Sylvester-Bradley 1948 emend Bate 1963

TYPE SPECIES. *Progonocythere stilla* Sylvester-Bradley.

***Progonocythere cristata* Bate**

1963 *Progonocythere cristata* Bate : 191, pl. 4, figs. 5-15, pl. 5, figs. 1-6.

REMARKS. Several poorly preserved specimens of this species have been found in the Hydraulic Limestone of Ellerker and in the Firby road section. At the equivalent horizon in Lincolnshire (Kirton Cementstone Series) the ostracod is also uncommon. The species becomes increasingly numerous at higher horizons, being well represented within the Kirton Shale at the type locality (Kirton Lindsey).

***Progonocythere reticulata* sp. nov.**

(Pl. 1, figs. 7-13, Pl. 2, figs. 1-11)

DERIVATION OF NAME. Latin, *reticulatus*, net-like.

DIAGNOSIS. A *Progonocythere* with carapace strongly reticulate.

HOLOTYPE. Io. 909, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 910-18, horizon and locality as above.

DESCRIPTION. *Carapace* subquadrate in the female dimorph, elongate in the male. Greatest length in both dimorphs extends through midpoint ; greatest height in the anterior third ; greatest width just behind midpoint. Ventrolateral margin of carapace convex, projected below the ventral surface, most strongly so in the male. In both sexes the greatest development of this ventrolateral extension is median, contrasting with the backwardly directed extension of the type species. *Shell surface* strongly reticulate, the ornamentation consisting of 4-5 sided pits. The size of the pits increases towards the centre of the carapace, those around the periphery being small and commonly circular in shape. Ventral surface of carapace with 4-5 weakly developed, longitudinal and parallel ridges on each valve. *Normal pore canals* well developed in the peripheral part of the valve, large and widely scattered. *Left valve* larger than the right, which it overreaches on all sides except at the extreme anterior. Along the ventral margin the left valve overlaps the right. Dorsal margin straight, sloping towards the posterior. Anterior cardinal angle broadly convex, posterior cardinal angle sharply angled. Posterior narrowly rounded, somewhat truncated, with a convex posteroventral slope and a concave posterodorsal slope. Anterior rounded, marginally compressed. Ventral margin convex, medially incurved. *Right valve* : dorsal margin slightly convex in the female, straight in the male, in both cases sloping to the posterior. Cardinal angles

distinct. Anterior rounded, marginally compressed, anterodorsal slope concave. Posterior triangular, posterodorsal slope strongly concave, posteroventral slope convex. Ventral margin convex, medially incurved. *Hinge* entomodont with a broad shelf-like accommodation groove in the left valve. Right valve with approximately 8 anterior teeth and 6-7 posterior teeth, the anterior element being continuous below the median groove. *Selva*ge most strongly developed midventrally. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* short and straight, widely spaced, approximately 8 anteriorly and 4 posteriorly. *Muscle scars* consist of a subvertical row of 4 oval adductor scars, an anterodorsal, oval antennal scar and a rounded anteroventral mandibular scar (Type A, Bate 1963).

Dimensions

Holotype. Io. 909 female carapace (Pl. 1, figs. 7, 9, 13) length 0.59 mm.; height 0.40 mm.; width 0.36 mm.

Paratypes. Io. 910 female L.V. (Pl. 1, figs. 8, 10, Pl. 2, fig. 11) length 0.55 mm.; height 0.40 mm. Io. 911 female R.V. (Pl. 2, fig. 7) length 0.60 mm.; height 0.39 mm. Io. 912 male carapace (Pl. 2, figs. 1, 3, 4) length 0.67 mm.; height 0.44 mm.; width 0.37 mm. Io. 913 male L.V. (Pl. 2, figs. 2, 8) length 0.65 mm.; height 0.41 mm. Io. 914 male R.V. (Pl. 2, fig. 6) length 0.64 mm.; height 0.39 mm. Io. 915 female R.V. (Pl. 1, fig. 11, Pl. 2, fig. 10) length 0.56 mm.; height 0.35 mm. Io. 916 female L.V. (Pl. 1, fig. 12) length 0.52 mm.; height 0.37 mm. Io. 917 male R.V. (Pl. 2, fig. 9) length 0.65 mm.; height 0.37 mm. Io. 918 male L.V. (Pl. 2, fig. 5) length 0.67 mm.; height 0.41 mm.

REMARKS. Apart from the occurrence of this species at the type locality, where it is a common ostracod, it has, so far, only been found elsewhere in the Hydraulic Limestone near Castle Howard station.

Genus **ACANTHOCY THERE** Sylvester-Bradley 1956 emend Bate 1963

TYPE SPECIES. *Cythere sphaerulata* Jones & Sherborn.

Subgenus **PROTOACANTHOCY THERE** Bate 1963

Acanthocythere (Protoacanthocythere) faveolata Bate

1963 *Acanthocythere (Protoacanthocythere) faveolata* Bate : 195, pl. 7, figs. 5-13, pl. 8, figs. 1-5.

REMARKS. A few specimens of this species occur in the marl facies of the Basement Beds, Eastfield Quarry, South Cave. So far this species has not been found elsewhere at this horizon in Yorkshire.

Genus **AULACOCY THERE** Bate 1963

TYPE SPECIES. *Aulacocythere punctata* Bate.

Aulacocythere punctata Bate

1963 *Aulacocythere punctata* Bate : 199, pl. 9, figs. 4-9, 11-12, 14-15.

REMARKS. Two specimens only of this species have been found at this horizon in Yorkshire in the Basement Beds (marl facies), Eastfield Quarry, South Cave.

Genus **MICROPNEUMATOCYTHERE** nov.

DERIVATION OF NAME. Greek μικρός, small, bearing a resemblance to the genus *Pneumatocythere* Bate 1963.

DIAGNOSIS. Carapace small, convex, with ventrolateral margin projecting strongly below ventral surface in side view. Left valve larger than right. Radial pore canals straight, widely spaced, and few in number. Hinge antimerodont. Muscle scars as for family (Type A).

TYPE SPECIES. *Micropneumatocythere convexa* sp. nov.

REMARKS. Through the kindness of Dr. G. A. Cooper (Smithsonian Institute) topotype material of *Procytheridea crassa* Peterson (1954, pl. 19, figs. 1-5) was examined. As previously stated (Bate 1963 : 214) this species is not congeneric with *P. exempla* Peterson (1954, pl. 19, figs. 6-14), the type species of *Procytheridea* Peterson 1954. Although the muscle scars were not discernible in the topotype material all other evidence points to the fact that *P. crassa* belongs in the genus *Micropneumatocythere*.

***Micropneumatocythere convexa* sp. nov.**

(Pl. 2, figs. 12-13, Pl. 3, figs. 1-15)

?1960 Ostracod No. 3. Lutze : 434, pl. 38, fig. 1a-b.

DERIVATION OF NAME. Latin, *convexus*, arched.

DIAGNOSIS. A *Micropneumatocythere* with carapace strongly convex in dorsal view, with coarse reticulate ornament.

HOLOTYPE. Io. 921, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 922-26, horizon and locality as above.

DESCRIPTION. Carapace oval in side view with the ventrolateral border extended below the ventral surface, the position of the overhang varying from almost median to posterior. Dorsal margin convex, ventral margin anteromedially incurved. Anterior broadly rounded ; posterior rounded triangular with a concave postero-dorsal slope and a convex posteroventral slope. Sexual dimorphism well developed, the presumed males being the more elongate. Greatest length passes through midpoint ; greatest height at or slightly in front of valve middle whilst the greatest width occurs at or just behind valve middle. Shell surface strongly reticulate. Ventral surface of each valve possesses 4 or 5 longitudinal ridges. Normal pore canals large, only clearly seen around the periphery of the carapace. Left valve larger than the right, which it overlaps along the ventral margin, slightly along the anterodorsal and posterodorsal slopes, and overreaches anteriorly and mid-dorsally. Right valve with a strongly concave posterodorsal slope, the posterior being almost upturned, overreaching the left valve at this point. Hinge antimerodont, left valve with a broad shelf-like accommodation groove ; right valve with 7 terminal teeth. Muscle scars (Type A, Bate 1963) situated anterior to valve

centre consisting of a vertical row of 4 oval adductor scars with a single, rounded anterodorsal antennal scar and a single, rounded anteroventral mandibular scar. The position of the antennal scar varies slightly in the individual, although basically anterodorsal it may approach an anteromedian position. *Inner margin* and *line of concrescence* coincide; *radial pore canals* short and straight, widely spaced, approximately 9 anteriorly and 3 posteriorly.

Dimensions

Holotype. Io. 921 female carapace (Pl. 3, figs. 1-4) length 0.51 mm.; height 0.34 mm.; width 0.32 mm.

Paratypes. Io. 922 male carapace (Pl. 3, figs. 5-7) length 0.60 mm.; height 0.36 mm.; width 0.33 mm. Io. 923 male R.V. (Pl. 3, figs. 11, 13-15) length 0.60 mm.; height 0.33 mm. Io. 924 male L.V. (Pl. 3, fig. 10) length 0.55 mm.; height 0.33 mm. Io. 925 female R.V. (Pl. 2, fig. 12, Pl. 3, fig. 8) length 0.43 mm.; height 0.25 mm. Io. 926 female L.V. (Pl. 2, fig. 13, Pl. 3, figs. 9, 12) length 0.48 mm.; height 0.32 mm.

REMARKS. This species occurs in the Hydraulic Limestone of Castle Howard and Ganthorpe and, more commonly, in the Basement Beds (marl facies), Eastfield Quarry, South Cave. In Lincolnshire it has been found in the Kirton Cementstone Series, Greetwell Quarry, Lincoln.

Although closely similar in outline to *Procytheridea crassa*, *M. convexa* differs noticeably in the following ways: greatest height median and not in the anterior third; more strongly convex in dorsal view, *P. crassa* tending to be almost parallel-sided; smaller in size, with a much more strongly swollen ventrolateral bulge. This species also closely resembles *Procytheridea reticulata* Klingler & Neuweiler (1959, pl. 14, figs. 19-21, 23-25), the latter is, however, almost parallel-sided in dorsal view with compressed anterior and posterior borders, characters not found in *M. convexa*. Ostracod No. 3, Lutze (1960, pl. 38, fig. 1a-b), most closely resembles this species and is tentatively placed in synonymy.

Genus **PNEUMATOCYTHERE** Bate 1963

TYPE SPECIES. *Pneumatocythere bajociana* Bate.

Pneumatocythere bajociana Bate

1963 *Pneumatocythere bajociana* Bate: 193, pl. 5, figs. 7-10, pl. 6, figs. 1-10, pl. 7, figs. 1-4.

REMARKS. *P. bajociana* occurs throughout South Yorkshire in the Hydraulic Limestone and associated marine sediments at all the localities examined.

Subfamily PLEUROCYTHERINAE Mandelstam 1960

Genus **PLEUROCYTHERE** Triebel 1951

TYPE SPECIES. *Pleurocythere richteri* Triebel.

Pleurocythere kirtonensis Bate

1963 *Pleurocythere kirtonensis* Bate : 203, pl. 10, figs. 14-18, pl. 11, figs. 1-5.

REMARKS. A single specimen of this species has been found in the Basement Beds (marl facies), South Cave. No other occurrence of this species in Yorkshire at this horizon has so far been noted.

Pleurocythere sp.

(Pl. 4, figs. 1-2)

REMARKS. A single right valve (Io. 928), length 0.55 mm.; height 0.27 mm., has been found in the Basement Beds (marl facies), Eastfield Quarry, South Cave, which agrees closely with the genus and is at the same time unlike any previously described species.

Family CYTHERIDEIDAE Sars 1925

Subfamily CYTHERIDEINAE Sars 1925

Genus **DOLOCY THERE** Mertens 1956

TYPE SPECIES. *Dolocythere rara* Mertens.

Dolocythere maculosa Bate

1963 *Dolocythere maculosa* Bate : 205, pl. 12, figs. 1-11.

REMARKS. An abundant species within the Basement Beds (marl facies), South Cave (the type locality). So far it has not been found elsewhere at this horizon in Yorkshire.

Genus **HOMOCY THERIDEA** nov.

DERIVATION OF NAME. Greek, ὁμος, uniform, + *cythereida*.

DIAGNOSIS. Elongate, parallel-sided, broadly rounded anteriorly and posteriorly. Hinge antimerodont. Muscle scars with crescentic anterodorsal antennal scar. Inner margin and line of concrescence coincide; radial pore canals few in number, straight and widely spaced.

TYPE SPECIES. *Homocytheridea cylindrica* sp. nov.

REMARKS. This genus, which is placed in the subfamily on account of shape, type of muscle scars (Type B, Bate 1963) and radial pore canals, differs from *Clithrocytheridea* Stephenson (1936) in the more uniform outline and fewer radial pore canals.

Homocytheridea cylindrica sp. nov.

(Pl. 4, figs. 3-11)

DERIVATION OF NAME. Latin, *cylindrus*, a cylinder.

DIAGNOSIS. A *Homocytheridea* with carapace cylindrical in outline, punctate.

HOLOTYPE. Io. 938, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 939-43, horizon and locality as above.

DESCRIPTION. Carapace elongate-oval with the greatest length passing through midpoint; greatest height in the anterior third; greatest width in the posterior

third. Dorsal and ventral margins almost parallel, sloping slightly to the posterior. Anterior broadly rounded; posterior narrower, also rounded. Ventral margin convex, incurved anteromedially. Dorsal margin convex in the right valve, almost straight in the left. Cardinal angles broadly rounded. *Shell surface* finely punctate. *Normal pore canals* large and widely spaced, rounded. Relationship of left to right valves is not known as a complete carapace has not been found. *Hinge* antimerodont, the median element in the left valve being a long, narrow, finely denticulate bar with no real accommodation groove above. 8 terminal teeth in the right valve. *Muscle scars* (Type B) consist of 4 oval adductor scars in a vertical row with a strongly crescentic anterodorsal antennal scar and an oval anteroventral mandibular scar. Dorsal muscle scars occur above the adductor scars (Pl. 4, fig. 7). *Inner margin* and *line of concrescence* coincide; *duplicature* of moderate width; *radial pore canals* straight, widely spaced, approximately 11 anteriorly and 4 posteriorly.

Dimensions

Holotype. Io. 938 L.V. (Pl. 4, figs. 3, 5, 9) length 0.81 mm.; height 0.43 mm.

Paratypes. Io. 939 R.V. (Pl. 4, figs. 4, 6, 10) length 0.85 mm.; height 0.42 mm. Io. 940 L.V. (Pl. 4, fig. 8) length 0.87 mm.; height 0.43 mm. Io. 941 L.V. (Pl. 4, figs. 7, 11) length 0.80 mm.; height 0.43 mm. Io. 942 R.V. length 0.79 mm.; height 0.38 mm. Io. 943 L.V. length 0.79 mm.; height 0.41 mm.

REMARKS. This species has so far been found only at the type locality. It does not occur in large numbers.

Genus **TETRACYTHERIDEA** nov.

DERIVATION OF NAME. Greek, τέτταρες, four, with reference to the outline of the carapace, + *cytheridea*.

DIAGNOSIS. Carapace angular subquadrate to subrectangular; thick shelled; dorsal margin straight or slightly convex; anterior and posterior margins rounded. Hinge antimerodont. Muscle scars with crescentic anterodorsal antennal scar. Radial pore canals few in number, straight or very slightly curved, widely spaced. Inner margin and line of concrescence coincide. Left valve larger than right.

TYPE SPECIES. *Tetracytheridea punctata* sp. nov.

REMARKS. *Tetracytheridea* has been placed in the subfamily Cytherideinae on general shape, type and arrangement of muscle scars (Type B) and simple radial pore canals. Although similar in outline to the genera *Asciocythere* Swain, *Schuleridea* Swartz & Swain, *Praeschuleridea* Bate and *Galliaecytheridea* Oertli, it differs from these by the arrangement of the muscle scars, the antennal scar being quite definitely anterodorsal in position, as opposed to an anteromedian position for the others, and in several cases by the possession of an antimerodont hinge. The dorsal margin, especially in the left valve, is typically straight in this genus, not nearly as convex as in the others.

***Tetracytheridea punctata* sp. nov.**

(Pl. 5, figs. 1-11, Pl. 6, figs. 1-2)

DERIVATION OF NAME. Latin, *punctum*, a small hole.

DIAGNOSIS. A *Tetracytheridea* with carapace punctate.

HOLOTYPE. Io. 944 Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 945-49, horizon and locality as above.

DESCRIPTION. *Carapace* subquadrate in outline, tapering posteriorly. Dimorphism indicated by the presence of a single elongate left valve which is considered to be the male. Greatest length passes through midpoint in both dimorphs; greatest height in the anterior third; greatest width behind midpoint. Ventro-lateral border slightly swollen, extended below the ventral surface. *Shell surface* finely punctate. *Normal pore canals* large, circular and widely spaced over the carapace. *Left valve* larger than the right, producing the typical subquadrate outline. The left valve overlaps the right in the region of the cardinal angles and along the ventral margin. Cardinal angles distinct. Dorsal margin straight, sloping steeply to the bluntly rounded posterior. Anterior uniformly rounded. Ventral margin with an anteromedian incurvature. *Right valve* oval in outline, tapering to the narrowly rounded posterior; anterior broadly rounded. Dorsal margin slightly convex; ventral margin incurved anteromedially. *Hinge* anti-merodont; coarsely loculate terminal sockets, dentate median bar with virtually no accommodation groove in the left valve. Right valve with 7-8 terminal teeth, the median loculate groove being slightly overhung by the dorsal edge of the valve. *Muscle scars* (Type B) consist of a vertical row of 4 oval adductor scars in front of which is a crescentic anterodorsal antennal scar and an oval or rounded antero-ventral mandibular scar. Several dorsal scars are situated above the adductor scars (Pl. 6, fig. 1). *Inner margin* and *line of concrescence* coincide; *duplication* moderate in width; *radial pore canals* very slightly curved, widely spaced, approximately 11 anteriorly and 5 posteriorly. *Selvage* most clearly developed along the ventral and posterior margins.

Dimensions

Holotype. Io. 944 female carapace (Pl. 5, figs. 1, 2, 6) length 0.67 mm.; height 0.43 mm.; width 0.37 mm.

Paratypes. Io. 945 female L.V. (Pl. 5, figs. 7, 10, 11) length 0.73 mm.; height 0.48 mm. Io. 946 female R.V. (Pl. 5, figs. 4, 5, 8) length 0.71 mm.; height 0.43 mm. Io. 947 male L.V. (Pl. 6, figs. 1, 2) length 0.79 mm.; height 0.43 mm. Io. 948 female R.V. (Pl. 5, fig. 9) length 0.66 mm.; height 0.41 mm. Io. 949 female R.V. (Pl. 5, fig. 3) length 0.73 mm.; height 0.45 mm.

REMARKS. This species has so far been found only at the type locality and in the marine shale underlying the Hydraulic Limestone on the Firby road.

The single left valve considered here to be a male dimorph is very similar to *Homocytheridea cylindrica* in outline but can be distinguished by the upward sweep of the posteroventral border, typical of this species, but not found in *H. cylindrica*.

The radial pore canals cannot be clearly distinguished in the male dimorph ; the duplicature is, however, not quite as broad as in the compared species.

Family SCHULERIDEIDAE Mandelstam 1959
Subfamily SCHULERIDEINAE Mandelstam 1959
Genus **ASCIOCYTHERE** Swain 1952

TYPE SPECIES. *Bythocypris rotundus* Vanderpool.

Asciocythere lacunosa sp. nov.
(Pl. 6, figs. 3-9, Pl. 7, figs. 1-6)

DERIVATION OF NAME. Latin, *lacunosus*, full of hollows.

DIAGNOSIS. An *Asciocythere* with carapace oval, greatest height median. Shell surface pitted. Hinge antimerodont.

HOLOTYPE. Io. 950, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 951-53, horizon and locality as above.

DESCRIPTION. *Carapace* oval in side view, rather inflated. Greatest length passes through midpoint ; greatest height and width median. *Shell surface* with large scattered pits of varying size ; poorly preserved specimens may appear smooth. *Left valve* larger than the right which it overreaches along the dorsal margin and slightly around the posterior margin. Ventrally the left valve overlaps the right. Dorsal margin convex, cardinal angles rounded. Ventral margin incurved medially. Anterior and posterior margins rounded. *Right valve* rather more subquadrate in outline than the left, with distinct cardinal angles and steeply sloping anterodorsal and posterodorsal margins. Dorsal margin slightly convex, ventral margin medially incurved. Anterior and posterior margins rounded. In both valves there is a slight midventral bulge as seen in lateral view. *Hinge* antimerodont ; the terminal sockets in the left valve are rather coarsely loculate, the dentate median bar is short and the accommodation groove shelf-like and well developed. Generally there are 7 anterior and 7 posterior teeth in the right valve, although a single specimen with 6 anterior and 8 posterior teeth has been observed ; median groove short and coarsely loculate. *Muscle scars* (Type C) with 4 rounded adductor scars situated in a crescent, just anterior of valve centre ; an oval or slightly kidney-shaped anteromedian antennal scar, in front of which may be a very small circular scar and an anteroventral mandibular scar, not, however, clearly seen. *Inner margin* and *line of concretion* coincide ; *duplicature* broad ; *radial pore canals* curved, arranged fan-like around the anterior margin, approximately 12 anteriorly, 4 posteriorly. *Selvage* well developed, particularly in the right valve.

Dimensions

Holotype. Io. 950 carapace (Pl. 6, figs. 3-6) length 0.71 mm. ; height 0.44 mm. ; width 0.36 mm.

Paratypes. Io. 951 L.V. (Pl. 6, figs. 7, 8, Pl. 7, fig. 5) length 0.80 mm.; height 0.49 mm. Io. 952 R.V. (Pl. 6, fig. 9, Pl. 7, figs. 1, 2, 4, 6) length 0.73 mm.; height 0.43 mm. Io. 953 R.V. (Pl. 7, fig. 3) length 0.73 mm.; height 0.41 mm.

REMARKS. This species has been found within the marine sediments which underlie the Hydraulic Limestone in the Firby road exposure as well as in the type locality. In Lincolnshire it is fairly common throughout the Lower Lincolnshire Limestone Greetwell Quarry, Lincoln, where it is, however, generally rather poorly preserved.

Genus ***EOCYTHERIDEA*** nov.

DERIVATION OF NAME. Greek, ἔως, early, + *cytheridea*.

DIAGNOSIS. Elongate-oval to subtriangular. Left valve larger than right. Hinge hemimerodont, anterior socket of left valve extending backwards below median bar as a narrow groove; accommodation groove poorly developed. Muscle scars as for family. Inner margin and line of concrescence coincide; radial pore canals long, slightly curved, approximately 14 in number anteriorly.

TYPE SPECIES. *Eocytheridea elongata* sp. nov.

REMARKS. The genus has been placed in the Schulerideinae on shape, muscle scars (Type C) and radial pore canals. In outline it is close to *Clithrococytheridea* Stephenson (1936), from which it differs in the possession of a reduced number of radial pore canals and the anteromedian position of the antennal scar. The genus can also be distinguished from *Homocytheridea* on the basis of muscle scars, radial pore canals and in the more distinctly tapered posterior.

It has been observed in both species described below that, where the hinge of the left valve has been subjected to wear, the groove extending below the median bar from the anterior socket appears to extend along the top of the bar.

Eocytheridea elongata sp. nov.

(Pl. 7, figs. 7-12, Pl. 8, figs. 1-5)

DERIVATION OF NAME. *Elongatus*, prolonged.

DIAGNOSIS. An *Eocytheridea* with carapace elongate, posteriorly tapered. Shell surface strongly ornamented with both large and small pits, roughly circular in shape. 14 slightly curved anterior radial pore canals and 4 posterior canals.

HOLOTYPE. Io. 954, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 955-59, horizon and locality as above.

DESCRIPTION. *Carapace* elongate, tapering to the posterior with the greatest length passing below midpoint; greatest height anterior of middle; greatest width below valve middle. *Shell surface* ornamented by roughly circular pits of two sizes: predominantly large pits inside of which a normal pore canal often opens and smaller, more numerous pits not apparently connected with pore canal openings. *Normal pore canals* most clearly seen around the periphery of the carapace; they do not appear to be very numerous over the central part of the valve.

Left valve larger than the right which it overlaps slightly along the ventral margin and overreaches along the dorsal margin. Dorsal margin convex, cardinal angles broadly rounded. Ventral margin incurved anteromedially. Anterior broadly rounded; posterior narrowly rounded. *Right valve* with a convex dorsal margin and rounded cardinal angles—the latter more noticeable than in the left valve. Ventral margin convex, incurved anteromedially. Anterior rounded; posterior tapering, narrowly rounded. In side view the ventral surface of each valve can be seen to possess a slight midventral swelling. *Hinge* hemimerodont, the anterior loculate socket of the left valve extending backwards, below the smooth median bar, only appearing to run along the bar in those specimens subjected to wear. Accommodation groove elongate and rather shallow. Right valve with approximately 7 anterior and 7 posterior teeth; the smooth median groove, slightly expanded anteriorly, is overhung by a long, narrow bar. *Muscle scars* (Type C) consist of a subvertical row of 4 oval adductor scars situated anterior of valve centre on the inside edge of a broad pit. An oval or slightly kidney-shaped antennal scar with a smaller scar in front is situated in an anteromedian position. The mandibular scar is anteroventrally situated. *Inner margin* and *line of concrescence* coincide; *duplicature* rather broad. *Radial pore canals* long, curved, 14 anteriorly and 4 posteriorly. *Selva* distinct. A small "lip" or triangular ledge is situated on the ventral surface of the right valve, below the anteromedian incurvature.

Dimensions

Holotype. Io. 954 R.V. (Pl. 7, figs. 8–10) length 0.91 mm.; height 0.47 mm.

Paratypes. Io. 955 L.V. (Pl. 7, figs. 7, 11, 12) length 0.81 mm.; height 0.44 mm. Io. 956 R.V. (Pl. 8, figs. 1, 2) length 0.97 mm.; height 0.49 mm. Io. 957 R.V. (Pl. 8, fig. 5) length 0.65 mm.; height 0.35 mm. Io. 958 carapace (Pl. 8, fig. 4) length 0.77 mm.; height 0.40 mm.; width 0.41 mm. Io. 959 L.V. (Pl. 8, fig. 3) length 0.67 mm.; height 0.35 mm.

REMARKS. The type locality is the only place where this species has been found.

Eocytheridea lacunosa sp. nov. (Pl. 8, figs. 6–11, Pl. 9, figs. 1–8)

DERIVATION OF NAME. Latin, *lacunosus*, full of hollows.

DIAGNOSIS. An *Eocytheridea* with carapace subquadrate to subrectangular, dimorphic. Shell surface coarsely pitted.

HOLOTYPE. Io. 960, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 961–64, horizon and locality as above and from the marine beds underlying the Hydraulic Limestone, Firby road exposure.

DESCRIPTION. *Carapace* subrectangular to subquadrate. Sexual dimorphism indicated by the presence of elongate (subrectangular) specimens which are here considered to be the males, the females being more subquadrate in outline. Greatest length passes through midpoint, greatest height in the anterior third, greatest width in the posterior third. *Left valve* larger than the right which it overlaps

along the ventral margin and in the region of the cardinal angles. Anteriorly and posteriorly the left valve slightly overreaches the right. Dorsal margin almost straight, cardinal angles distinct. Anterior and posterior margins rounded. Ventral margin medially incurved. *Right valve* with a slightly more marked posterior taper than the left and with a much more strongly convex dorsal margin, cardinal angles prominent. Anterior and posterior margins rounded, the latter more narrowly so. Ventral margin medially incurved with a triangular "lip" developed below. *Shell surface* ornamented with large, roughly circular pits with a subordinate number of smaller pits situated between, although in general all pits decrease in size towards the periphery. *Normal pore canals* most common around the outer margin of the carapace. *Hinge* hemimerodont, the anterior socket of the left valve continued below the smooth median bar as a narrow groove. Accommodation groove in this valve, elongate. Right valve with 6-7 terminal teeth. Median groove smooth, slightly expanded anteriorly and overhung by a long, narrow bar. *Muscle scars* (Type C) consist of a vertical row of 4 oval adductor scars with a single, anteromedian, slightly kidney-shaped antennal scar. So far a mandibular scar has not been observed. *Inner margin* and *line of concrescence* coincide; *duplicature* fairly broad; *radial pore canals* long, slightly curved and splayed out around the anterior margin; 14 anterior and 4 posterior canals observed.

Dimensions

Holotype. Io. 960 female carapace (Pl. 8, figs. 6, 8, 9) length 0.69 mm.; height 0.41 mm.; width 0.33 mm.

Paratypes. Io. 961 male carapace (Pl. 9, figs. 1-4) length 0.79 mm.; height 0.43 mm.; width 0.35 mm. Io. 962 female R.V. (Pl. 9, figs. 7, 8) length 0.67 mm.; height 0.35 mm. Io. 963 male L.V. (Pl. 9, figs. 5, 6) length 0.74 mm.; height 0.39 mm. Io. 964 male R.V. (Pl. 8, figs. 7, 10, 11) length 0.77 mm.; height 0.36 mm.

REMARKS. *Eocytheridea lacunosa* differs from the type species in being smaller, dimorphic and not so elongate in outline. It is also much more common in the sediments examined, being found not only at South Cave in the Basement Beds, but also in the marine sequence below the Hydraulic Limestone in the Firby road exposure, and approximately 10 ft. from the top of the Kirton Cementstone Series as exposed in the Greetwell Quarry, Lincoln.

Genus **PARASCHULERIDEA** Swartz & Swain 1946

TYPE SPECIES. *Paraschuleridea anumbonata* Swartz & Swain.

REMARKS. The genus is placed in the family Schulerideidae, subfamily Schulerideinae, on shape and type of muscle scars present. The radial pore canals exhibited in the species described below are short, tending to enlarge at their base. It may well be that the genus will eventually be placed in a new subfamily on this latter evidence.

Paraschuleridea ornata sp. nov.

(Pl. 9, figs. 9-12, Pl. 10, figs. 1-3; Text-fig. 2)

DERIVATION OF NAME. Latin, *ornatus*, decorated.

DIAGNOSIS. A *Paraschuleridea* with carapace ornamented with large circular pits which decrease in size away from valve centre. In central part of valve pits are aligned in rows between transverse ridges, the latter diverging outwards from dorsal margin.

HOLOTYPE. Io. 965, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 966-70, horizon and locality as above.

DESCRIPTION. Carapace subovate in outline, tapering to the posterior. Greatest length through midpoint; greatest height in the anterior third. Shell surface strongly ornamented with circular pits, increasing in size towards valve centre where they lie between prominent transverse ridges, the latter diverging outwards from the dorsal margin. In both valves there is a low, elongate swelling situated in the region of the anterior cardinal angle, below which there is a shallow, oblique furrow. Normal pore canals large, particularly well seen around the periphery of the valve. Left valve oval in outline; dorsal margin straight or slightly convex, sloping to the posterior. Anterior cardinal angle rounded, posterior angle rather more acute. Ventral margin medially incurved. Anterior margin compressed. Right valve slightly more angular in outline, particularly in the case of the cardinal angles. Dorsal margin convex; ventral margin medially incurved. Anterior broadly rounded, compressed; posterior triangular with a rather steep, slightly concave posterodorsal slope and a convex posteroventral slope. Hinge hemimerodont; left valve with rather elongate loculate sockets and a narrow, smooth bar above which there is an elongate accommodation groove. In the right valve there are approximately 5 anterior and 5 posterior teeth separated by a long, narrow, smooth groove. Inner margin and line of concrescence coincide; duplicature narrow; radial pore canals short, somewhat triangular in outline, widening towards

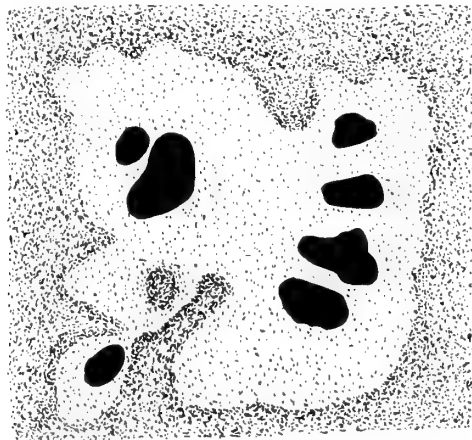


FIG. 2. Camera lucida drawing, muscle scars, *Paraschuleridea ornata* sp. nov., paratype Io. 969, $\times 470$ approx.

the inner margin, anterior canals splayed out around the anterior margin. Approximately 11 anterior and 6 posterior canals. *Muscle scars* (Type C) consist of a subvertical row of 4 oval adductor scars, an anteromedian kidney-shaped antennal scar, the latter with a small circular scar in front, and a circular, anteroventral mandibular scar (Text-fig. 2). Above these there is a group of dorsal scars, the importance of which has not yet been ascertained.

Dimensions

Holotype. Io. 965 L.V. (Pl. 9, figs. 9, 11, 12) length 0.63 mm.; height 0.37 mm.

Paratypes. Io. 966 R.V. (Pl. 9, fig. 10, Pl. 10, figs. 1, 2) length 0.63 mm.; height 0.36 mm. Io. 967 L.V. length 0.65 mm.; height 0.39 mm. Io. 968 R.V. (Pl. 10, fig. 3) length 0.55 mm.; height 0.33 mm.

REMARKS. This species has so far been found only in the Basement Beds (marl facies), Eastfield Quarry, where it occurs (isolated valves only) in large numbers.

Paraschuleridea sp.

(Pl. 10, figs. 4-7)

REMARKS. Two single valves, similar in appearance to *P. ornata* have been found in the Basement Beds (marl facies), Eastfield Quarry, South Cave. Both valves are coarsely pitted but are slightly more elongate than, and without the transverse ridges of *P. ornata*.

Dimensions

Io. 971 R.V. (Pl. 10, figs. 6, 7) length 0.59 mm.; height 0.31 mm. Io. 972 L.V. (Pl. 10, figs. 4, 5) length 0.61 mm.; height 0.35 mm.

Genus *PRAESCHULERIDEA* Bate 1963

TYPE SPECIES. *Cytheridea subtrigona*, Jones & Sherborn.

Praeschuleridea ventricosa ventricosa (Plumhoff)

(Pl. 10, figs. 8-13, Pl. 11, figs. 1-9, Pl. 12, figs. 1-4, 7, 8)

1963 *Procytheridea* ? *ventricosa ventricosa* Plumhoff : 36, pl. 6, figs. 95-98.

DIAGNOSIS. A *Praeschuleridea* characterized by strong, transverse ridges, which in a few cases bifurcate at about valve centre, and large 5-6 sided pits arranged in rows parallel to ridges.

MATERIAL. Over 100 specimens from the Basement Beds (marl facies), Eastfield Quarry, South Cave. Registered Io. 973-82 and Io. 1219.

DESCRIPTION. *Carapace* oval in outline, strongly dimorphic, the presumed males being the more elongate. Greatest length passes through midpoint; greatest height slightly anterior of midpoint; greatest width median. *Shell surface* strongly ornamented with transverse ridges which radiate outwards from the dorsal margin and which may bifurcate at about valve centre. Large, 5-6 sided or rounded pits

are arranged in rows parallel to the ridges. The size of the pits decreases towards the periphery of the valve. *Normal pore canals* large, opening at the surface as circular pits, only clearly seen around the periphery of the carapace. *Left valve* larger than the right, which it overreaches on all sides except midventrally, where the left overlaps the right. Dorsal margin convex with rounded cardinal angles. Anterior and posterior rounded. Ventrolateral margin broadly convex; ventral margin anteromedially incurved. *Right valve* with more sharply angled cardinal angles. An oblique swelling is also situated on this valve, below the anterior cardinal angle. Associated with the swelling is an oblique furrow situated beneath. Anterior rounded; posterior rather triangular with a short and very steeply inclined posterodorsal slope and a convex posteroventral slope. Dorsal margin convex; ventrolateral margin broadly convex, overlapping the ventral surface, particularly midventrally. Ventral margin incurved anteromedially. Both valves possess an anterior marginal furrow which has the effect of producing a marginal rim. *Hinge* paleohemimerodont, with, in the left valve, terminal loculate sockets and a smooth median groove upraised across a smooth median bar. Accommodation groove broad and shelf-like. Right valve with 6-7 anterior and 7-8 posterior teeth, separated by a smooth median groove, across which the teeth are connected by a low ridge. *Inner margin* and *line of concrescence* coincide; *duplication* broad; *radial pore canals* widely spaced and splayed out, fan-like, around the anterior margin, in which region there are 12 in number. Posteriorly there are approximately 4 pore canals. *Selva* prominent; a narrow *flange* is present around the anterior margin of both valves. *Muscle scars* (Type C) consist of a crescent of 4 oval adductor scars with a kidney-shaped anteromedian antennal scar, in front of which there is a smaller, oval scar. Mandibular scar, usually oval, occupies an anteroventral position. Dorsal muscle scars are situated close to the hinge and occur directly above the adductor scars.

Dimensions

Io. 973 male carapace (Pl. 10, figs. 10, 12, 13) length 0.88 mm.; height 0.52 mm.; width 0.36 mm. Io. 974 female L.V. (Pl. 11, figs. 3, 6, Pl. 12, fig. 7) length 0.68 mm.; height 0.47 mm. Io. 975 female R.V. (Pl. 12, figs. 1, 2, 8) length 0.67 mm.; height 0.43 mm. Io. 976 female carapace (Pl. 11, figs. 2, 4, 5) length 0.68 mm.; height 0.45 mm.; width 0.37 mm. Io. 977 male L.V. (Pl. 10, fig. 8, Pl. 11, fig. 8) length 0.78 mm.; height 0.49 mm. Io. 978 male R.V. (Pl. 10, fig. 9, Pl. 11, figs. 7, 9) length 0.85 mm.; height 0.47 mm. Io. 979 female R.V. length 0.63 mm.; height 0.41 mm. Io. 980 male L.V. (Pl. 10, fig. 11, Pl. 11, fig. 1) length 0.88 mm.; height 0.49 mm. Io. 981 male R.V. (Pl. 12, fig. 4) length 0.56 mm.; height 0.31 mm.

REMARKS. *P. ventricosa ventricosa* occurs in large numbers within the marl facies of the Basement Beds, Eastfield Quarry, and is also common in the marine sediments underlying the Hydraulic Limestone in the Firby road section. A loose block of the Hydraulic Limestone collected at Ganthorpe also contained examples of this species. In Lincolnshire, several specimens have been found at about the centre of the Kirton Cementstone sequence, Greetwell Quarry, Lincoln.

In outline and ornamentation this species approaches *Paraschuleridea ornata*,

from which it can, however, be distinguished by the hinge, radial pore canals, much coarser ornamentation, presence of strong dimorphism and the absence of the prominent posterior taper, characteristic of the latter.

***Praeschuleridea subtrigona* (Jones & Sherborn)**

1888 *Cytheridea subtrigona* Jones & Sherborn : 265, pl. 2, fig. 9a-c.

1963 *Praeschuleridea subtrigona* (Jones & Sherborn) Bate : 207, pl. 12, figs. 12-16, pl. 13, figs. 1-9.

REMARKS. This species occurs within the Hydraulic Limestone facies of Ellerker, Castle Howard station, Ganthorpe and Firby road. At the latter locality it is also common within the underlying marine shale and sandstone. So far this species has not been found in the marl facies of the Basement Beds.

Family CYTHERURIDAE Müller 1894

Genus **CYTHEROPTERINA** Mandelstam 1956

TYPE SPECIES. *Cytheropterina vegranda* [*sic*] Mandelstam.

REMARKS. Although placed in synonymy with the genus *Orthonotacythere* Alexander 1933 (*in* Moore 1961 : Q 296), the genus is considered to be valid and distinguishable from the former by shape (here the presence of strong ventrolateral alar extensions of the carapace are important) and absence of a tubercular ornament. The genus is placed tentatively in the family Cytheruridae on shape of carapace.

***Cytheropterina comica* sp. nov.**
(Pl. 12, figs. 5-18)

DERIVATION OF NAME. Latin, *comicus*, -a, -um, in allusion to the clown's mouth ornamentation on the ala.

DIAGNOSIS. A *Cytheropterina* with deeply sculptured alaeform extension of ventrolateral margin, each ala possessing a large crescent-shaped furrow, producing the "clown's mouth" allusion.

HOLOTYPE. Io. 990, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 991-97, horizon and locality as above, including material from the Kirton Cementstone Series, Greetwell Quarry, Lincoln.

DESCRIPTION. *Carapace* ovoid in outline with a well developed alaeform projection of the ventrolateral margin and a short, upturned, caudal process. Greatest length, height and width median. Sexual dimorphism indicated by the presence of more elongate specimens considered to be males. *Shell surface* ornamented with an irregular series of furrows and ridges. A deep, almost S-shaped transverse furrow is situated at valve centre. The alae are deeply incised by two crescentic furrows, the uppermost of which is rather wide and gives the allusion referred to in the specific name. The lowermost of the two furrows parallels the ventral margin

of the ala. The ventral surface of each valve is ornamented with 3-4 longitudinal ridges, this ornament is absent in some specimens. *Normal pore canals* large, few in number and widely spaced, only clearly seen around the ventral margin of the alae. *Left valve* larger than the right which it overreaches along the dorsal margin and around the anterior. Ventrally the left valve slightly overlaps the right. Outline ovoid with convex dorsal and ventral margins, the latter possessing a shallow anteromedian incurvature. Cardinal angles rounded. Anterior uniformly rounded, posterior triangular, slightly upturned; posterodorsal slope strongly concave, posteroventral slope convex. *Right valve* similar in outline, the cardinal angles tend, however, to be more prominent. *Hinge* antimerodont with terminal loculate sockets, a finely denticulate median bar and a broad, shelf-like accommodation groove in the left valve. Right valve with approximately 6 terminal teeth and a median groove, not well preserved in the material examined, but presumably locellate. *Inner margin* and *line of concrescence* coincide; *radial pore canals* straight and widely spaced, 7 in number anteriorly and 5 posteriorly. *Muscle scars* (Type A) consist of a vertical row of 4 oval adductor scars situated anteriorly of midpoint, with a single, oval, anterodorsal antennal scar and a rounded anteroventral mandibular scar. *Selvae* distinct.

Dimensions

Holotype Io. 990 female L.V. (Pl. 12, figs. 9, 10) length 0.45 mm.; height 0.31 mm.

Paratypes. Io. 991 female carapace (Pl. 12, figs. 11-14) length 0.42 mm.; height 0.27 mm.; width 0.31 mm. Io. 992 female carapace length 0.41 mm.; height 0.28 mm.; width 0.25 mm. Io. 993 male L.V. (Pl. 12, figs. 5, 6, 15) length 0.52 mm.; height 0.32 mm. Io. 994 male L.V. (Pl. 12, figs. 16, 18) length 0.53 mm.; height 0.35 mm. Io. 995 female R.V. length 0.40 mm.; height 0.28 mm. Io. 996 male R.V. (Pl. 12, fig. 17) length 0.52 mm.; height 0.31 mm.

REMARKS. This species occurs not only in the marl facies of the Basement Beds (where it is the most abundant) but also in the Hydraulic Limestone of Ganthorpe and Firby road and in the Kirton Cementstone Series of Lincoln. It is not, however, common or particularly well preserved in the latter sediments.

Cytheropterina gravis sp. nov.

(Pl. 13, figs. 1-10)

DERIVATION OF NAME. Latin, *gravis*, serious, pertaining to the thin, incised furrow on the ala.

DIAGNOSIS. *Cytheropterina* with weakly ornamented carapace; transverse wrinkles at valve centre, narrow crescentic furrow on each ala.

HOLOTYPE. Io. 998, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPES. Io. 999-Io. 1004, horizon and locality as above, including material from the Kirton Cementstone Series, Greetwell Quarry, Lincoln.

DESCRIPTION. *Carapace* oval in outline with a short, upturned caudal process and a ventrolateral alar extension. Greatest length, height and width median. Sexual dimorphism indicated by the presence of elongate specimens, considered

to be the males. *Shell surface* weakly ornamented with transverse wrinkles, and a deeply incised central furrow. A narrow, crescentic furrow extends across the base of each ala, approximately paralleling the outline of the structure. *Left valve* larger than the right which it overlaps along the ventral margin, but overreaches dorsally. Dorsal margin broadly convex, cardinal angles indistinct. Ventral margin convex with a shallow, anteromedian incurvature. Ventrolateral margin extended to form an alae-form process which projects below the ventral surface. Anterior broadly rounded, posterior bluntly triangular, upturned. Posterodorsal slope strongly concave, posteroventral slope convex. *Right valve* similar in outline, but with more prominent cardinal angles. *Hinge* antimerodont, with terminal loculate sockets, a finely denticulate median bar and a narrow accommodation groove in the left valve. Right valve with 6 anterior and 9 posterior teeth and a narrow median groove. *Muscle scars* (Type A) consist of a vertical row of 4 oval adductor scars, a single, rounded, anterodorsal antennal scar and a single, rounded anteroventral mandibular scar. *Inner margin and line of concrescence* coincide; *radial pore canals* not clearly seen but anteriorly appear to consist of 4-5 straight, widely spaced canals.

Dimensions

Holotype. Io. 998 male L.V. (Pl. 13, figs. 1, 2, 7) length 0.57 mm.; height 0.37 mm.

Paratypes. Io. 999 female R.V. (Pl. 13, figs. 3, 6, 8) length 0.41 mm.; height 0.28 mm. Io. 1000 female L.V. (Pl. 13, figs. 4, 5) length 0.43 mm.; height 0.29 mm. Io. 1001 female L.V. (Pl. 13, fig. 10) length 0.41 mm.; height 0.29 mm. Io. 1002 male L.V. (Pl. 13, figs. 9, 11) length 0.51 mm.; height 0.31 mm. Io. 1003 male L.V. length 0.54 mm.; height 0.33 mm. Io. 1004 male carapace length 0.53 mm.; height 0.32 mm.; width 0.36 mm.

REMARKS. *Cytheropterina gravis* differs from *C. comica* in the narrowness of the crescentic furrow situated at the base of the ala. It is this distinction which has given rise to the two specific names. The basic valvular ornamentation is weaker in the former species, which also tends to have a less prominent ala.

Apart from the type locality, where it is fairly common, *C. gravis* occurs in the marine strata underlying the Hydraulic Limestone, Firby road section, and throughout the Kirton Cementstone Series, Greetwell Quarry, Lincoln.

Family PROTOCYTHERIDAE Ljubimova 1955

Subfamily KIRTONELLINAE Bate 1963

Genus **KIRTONELLA** Bate 1963

TYPE SPECIES. *Kirtonella plicata* Bate.

Kirtonella plicata Bate

1963 *Kirtonella plicata* Bate : 210, pl. 13, figs. 10-19, pl. 14, figs. 1-6, 11-12.

REMARKS. A single male carapace has been found within the Hydraulic Limestone facies, Firby road.

Genus **EKTYPHOCYTHERE** Bate 1963TYPE SPECIES. *Procytheridea triangula* Brand.***Ektyphocythere triangula*** (Brand)1961 *Procytheridea triangula* Brand : 161, pl. 1, figs. 11-14.1963 *Ektyphocythere triangula* (Brand) Bate : 214, pl. 15, figs. 5-18.

REMARKS. The lowest horizon at which this species has been found in Yorkshire is the Hydraulic Limestone, in which it occurs at Ellerker, Firby road and Ganthorpe. At South Cave the species occurs in the overlying marl facies of the Basement Beds.

Genus **KINKELINELLA** Martin 1960TYPE SPECIES. *Kinkelinella tenuicostati* Martin.***Kinkelinella ? bajociana*** sp. nov.

(Pl. 13, figs. 12-19)

DIAGNOSIS. Like *Kinkelinella* with shell surface finely pitted, almost smooth. Radial pore canals straight, approximately 8 anteriorly ; inner margin and line of concrescence coinciding. Muscle scars with V-shaped anterodorsal antennal scar. Left valve larger than right.

HOLOTYPE. Io. 1008, Basement Beds (marl facies), Eastfield Quarry, South Cave.

PARATYPE. Io. 1009, horizon and locality as above.

DESCRIPTION. *Carapace* subquadrate in outline, tapering slightly to the posterior. Dorsal margin very slightly convex, almost straight ; cardinal angles rounded. Ventrolateral margin convex. Ventral margin incurved posteromedially. Anterior broadly rounded ; posterior narrowly rounded. Greatest length through midpoint ; greatest height in the anterior third ; greatest width median. *Shell surface* ornamented with shallow, irregular-sided pits producing an almost reticulate appearance, but only weakly so. *Normal pore canals* large and widely scattered. Left valve larger than the right, which it overlaps along the ventral margin, particularly midventrally, and in the region of the antero- and posterodorsal slopes. Anteriorly the left valve overreaches the right. Only in the *right valve* have the internal details been observed. *Hinge* hemimerodont with 5 anterior and 6 posterior teeth. Median groove smooth and elongate. *Inner margin* and *line of concrescence* coincide ; *duplication* quite broad ; *radial pore canals* not clearly seen but appear to be slender, straight and widely spaced, approximately 8 anteriorly, not seen posteriorly. *Muscle scars* consist of a vertical row of 4 oval adductor scars with a V-shaped anterodorsal antennal scar and a rounded, anteroventral mandibular scar (Type D).

Dimensions

Holotype. Io. 1008 carapace (Pl. 13, figs. 12-16) length 0.53 mm.; height 0.32 mm.; width 0.27 mm.

Paratype. Io. 1009 R.V. (Pl. 13, figs. 17-19) length 0.48 mm.; height 0.29 mm.

REMARKS. The genus *Kinkelina* was erected by Martin (1960) for a single species, *K. tenuicostata*, which occurs in the Liassic *Dactylioceras tenuicostatum* Zone of Germany. In shape, hinge and radial pore canals *K. ? bajociana* agrees closely with the characters of the genus. However, the assignment of the present species to the genus is only tentative at the moment because of the lack of knowledge concerning the muscle scars of the type species. Certainly the muscle scars as exhibited by *K. ? bajociana*, together with the hemimerodont hinge, are sufficient to distinguish this genus from other genera present within the Lower and Middle Jurassic sediments, which possess a superficial external resemblance.

Genus **SYSTEMOCYTHERE** Bate 1963

TYPE SPECIES. *Systemocythere exilofasciata* Bate.

Systemocythere exilofasciata Bate

1963 *Systemocythere exilofasciata* Bate : 212, pl. 14, figs. 7-10, 13-17, pl. 15, figs. 1-4.

REMARKS. A single male carapace (Io. 615, figured, Bate 1963, pl. 14, figs. 14, 15) has been found in the Basement Beds (marl facies), Eastfield Quarry, South Cave. It has not been recorded from any other locality.

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IV. APPENDIX

While the present paper was in press, two publications (listed below) appeared in which Middle Jurassic Ostracoda were described from Germany. Of these the more immediately important is that of Plumhoff, who describes and figures the ostracod *Procytheridea ? ventriosa*, attributing the species to "Fischer (in press)". It is of course Plumhoff's species.

The type subspecies is here referred to the genus *Praeschuleridea*, although space did not permit the listing of a complete synonymy. The synonymies of other species affected are being brought up to date in a paper on the Middle Jurassic Ostracoda of Yorkshire.

- PLUMHOFF, F. 1963. Die Ostracoden Oderaalenium und tiefen Unterbajocium (Jura) des Gifhorner Troges, Nordwestdeutschland. *Abh. Senckenb. naturf. Ges.*, Frankfurt a.M., **503** : 1-100, pls. 1-12.
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EXPLANATION OF PLATES

All specimens $\times 85$ unless otherwise indicated. Specimens coated with silver nitrate before photographing. Muscle scars and radial pore canals photographed with the specimen immersed in glycerine. Except where otherwise stated, all specimens are from the Basement Beds, South Cave, Yorkshire.

PLATE 1

- Cytherelloidea eastfieldensis* sp. nov. p. 25
- FIG. 1. External view, right valve, paratype Io. 901.
- FIGS. 2-5. Left, right, dorsal and ventral views, holotype Io. 900.
- Monoceratina vulsa* (Jones & Sherborn) p. 26
- FIG. 6. Internal view, left valve, Io. 541.
- Progonocythere reticulata* sp. nov. p. 27
- FIGS. 7, 9, 13. Right, dorsal and ventral views, female holotype Io. 909.
- FIGS. 8, 10. External and dorsal views, left valve, female paratype Io. 910.
- FIG. 11. Dorsal view, right valve, female paratype Io. 915.
- FIG. 12. External view, left valve, female, showing normal pore canals, paratype Io. 916.

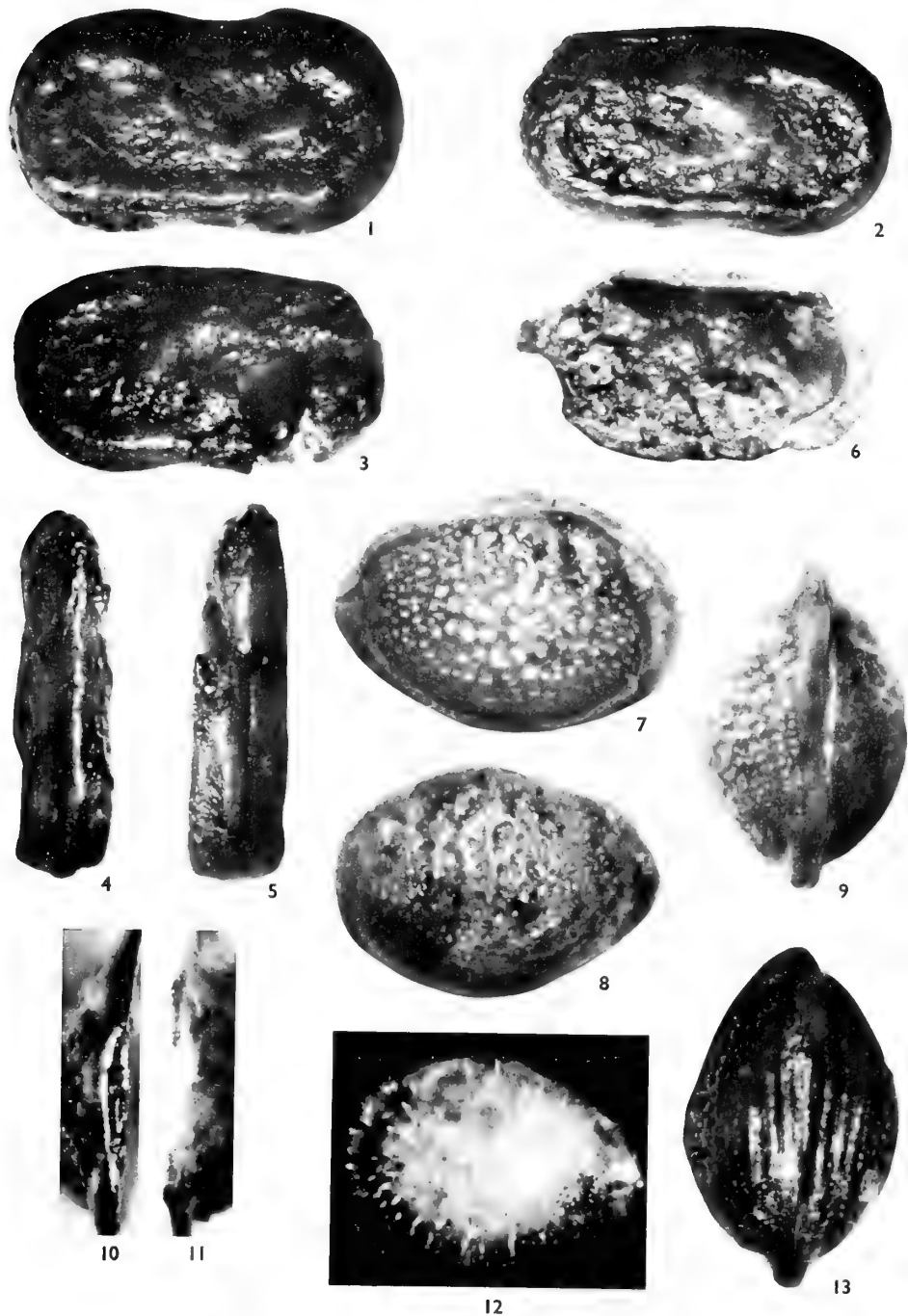




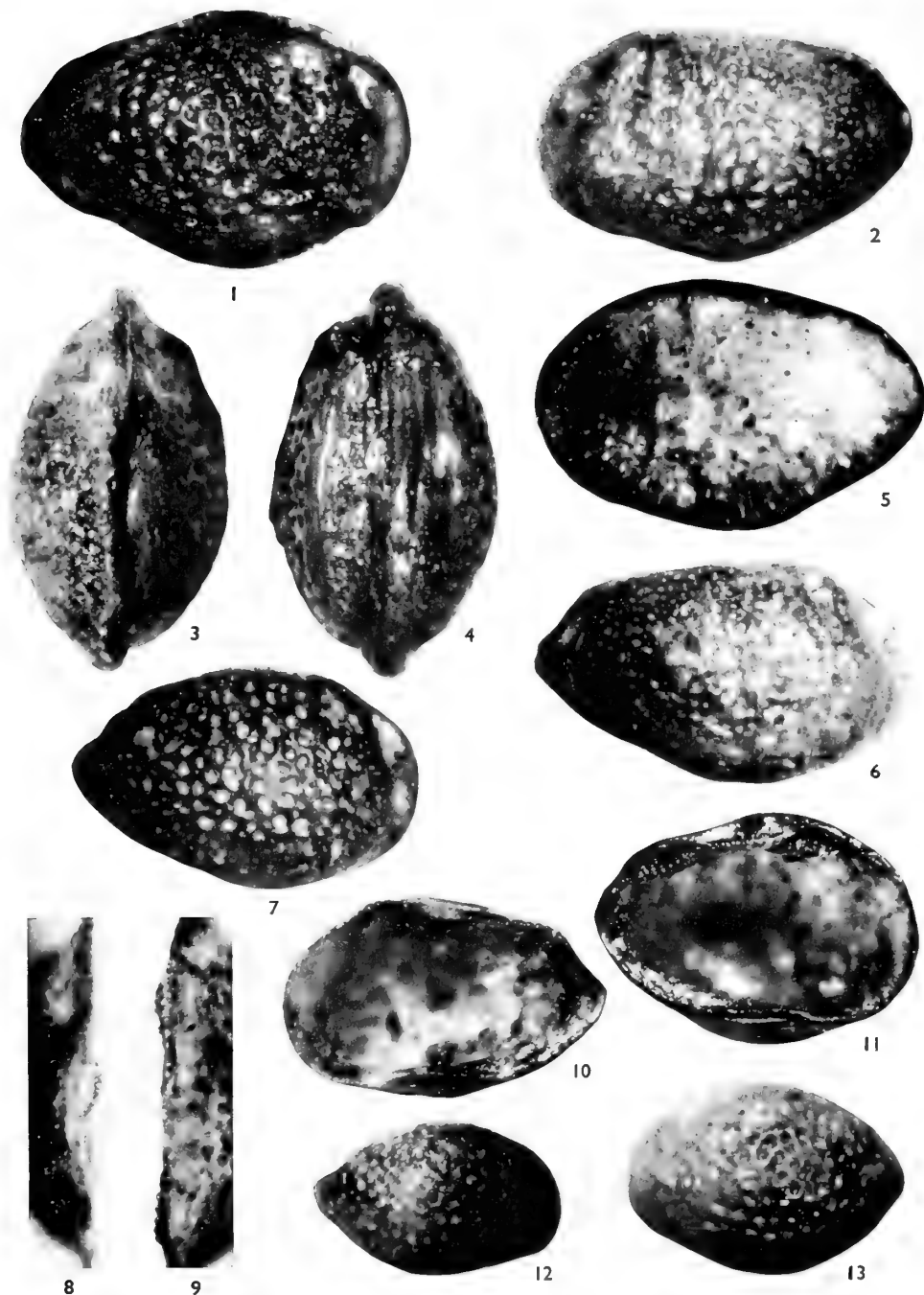
PLATE 2

Progonocythere reticulata sp. nov. p. 27

- FIGS. 1, 3, 4. Right, dorsal and ventral views, male paratype Io. 912.
FIGS. 2, 8. External and dorsal views, left valve, male paratype Io. 913.
FIG. 5. External view showing muscle scars, left valve, male paratype Io. 918.
FIG. 6. External view, right valve, male paratype Io. 914.
FIG. 7. External view, right valve, female paratype Io. 911.
FIG. 9. Dorsal view, right valve, male paratype Io. 917.
FIG. 10. Internal view, right valve, female paratype Io. 915.
FIG. 11. Internal view, left valve, female paratype Io. 910.

Micropneumatocythere convexa gen. et sp. nov. p. 29

- FIG. 12. External view, right valve, female paratype Io. 925.
FIG. 13. External view, left valve, female paratype Io. 926.



PROGONOCY THERE, MICROPNEUMATOCY THERE





PLATE 3

Micropneumatocythere convexa gen. et sp. nov. p. 29

FIGS. 1-4. Right, left, ventral and dorsal views, female holotype Io. 921.

FIGS. 5-7. Right, left and dorsal views, male paratype Io. 922.

FIG. 8. Internal view, right valve, female paratype Io. 925.

FIGS. 9, 12. Internal and dorsal views, left valve, female paratype Io. 926.

FIG. 10. Internal view, left valve, male paratype Io. 924.

FIGS. 11, 13-15. Muscle scars, dorsal and internal views showing hinge, muscle scars and radial pore canals, (fig. 11 $\times 300$) right valve, male paratype Io. 923.

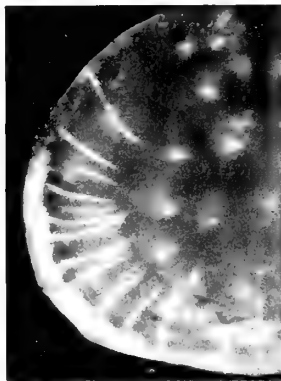
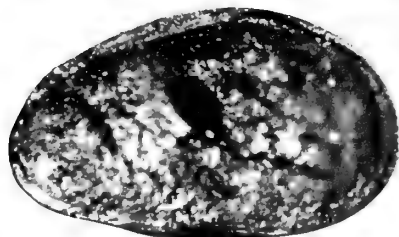
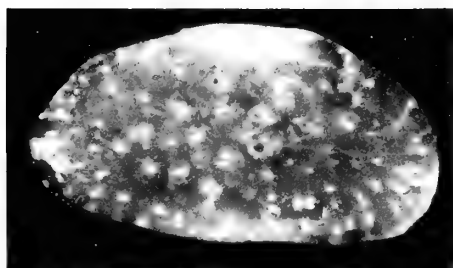
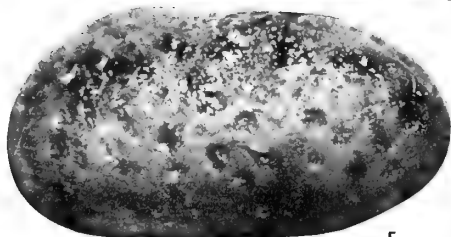
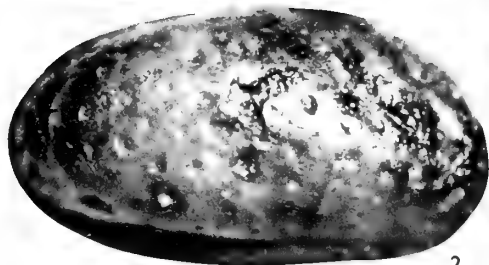
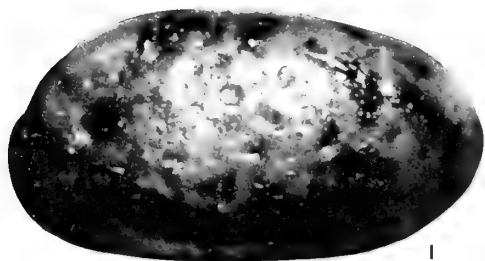
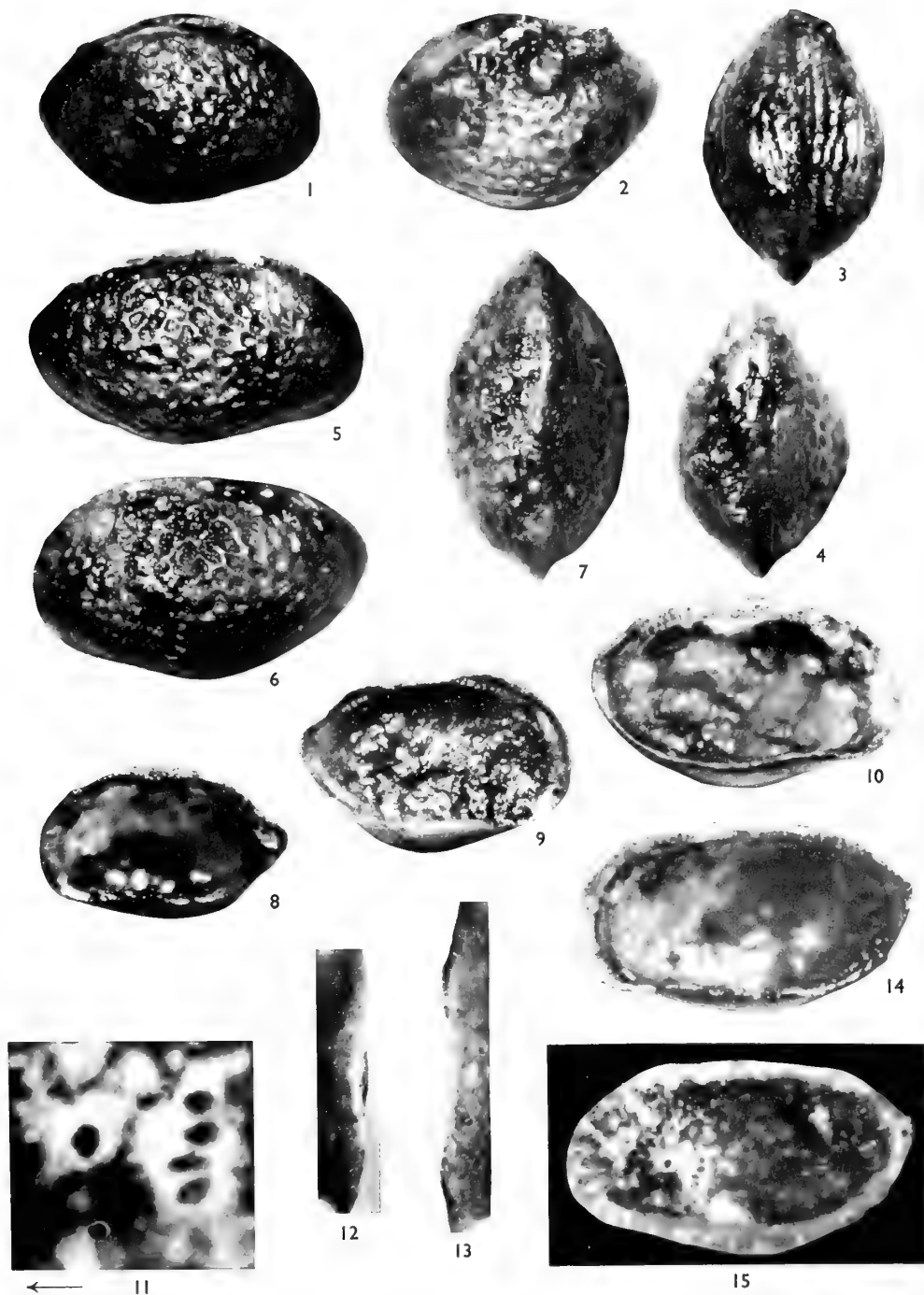






PLATE 10

- Paraschuleridea ornata* sp. nov. p. 37
- FIGS. 1, 2. Internal and external views, right valve, paratype Io. 966.
- FIG. 3. Radial pore canals (slightly retouched), right valve, paratype Io. 968 \times 135.
- Paraschuleridea* sp. p. 39
- FIGS. 4, 5. External and internal views, left valve, Io. 972.
- FIGS. 6, 7. External and internal views, right valve, Io. 971.
- Praeschuleridea ventricosa ventricosa* (Plumhoff) p. 39
- FIG. 8. Dorsal view, left valve, male paratype Io. 977.
- FIG. 9. Dorsal view, right valve, male paratype Io. 978.
- FIGS. 10, 12, 13. Right, dorsal and ventral views, male holotype Io. 973.
- FIG. 11. External view, left valve, male paratype Io. 980 \times 73.



MICROPNEUMATOCY THERE

PLATE 4

Pleurocythere sp. p. 31

FIGS. 1, 2. External and internal views, right valve, Io. 928.

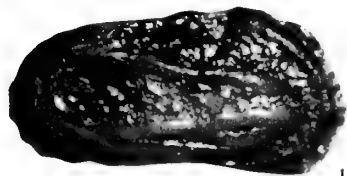
Homocytheridea cylindrica gen. et sp. nov. p. 31

FIGS. 3, 5, 9. External (showing muscle scars), internal and dorsal views, left valve, holotype Io. 938.

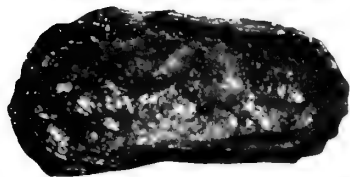
FIGS. 4, 6, 10. Internal, external and dorsal views, right valve, paratype Io. 939.

FIGS. 7, 11. Muscle scars, Fig. 7 $\times 235$, showing dorsal scars, adductor and antennal scars, internal view of valve; Fig. 11 $\times 245$, showing adductor, antennal and mandibular scars, external view of valve, left valve paratype Io. 941.

FIG. 8. Radial pore canals, left valve paratype Io. 940 $\times 144$.



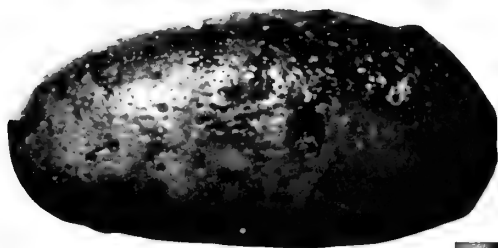
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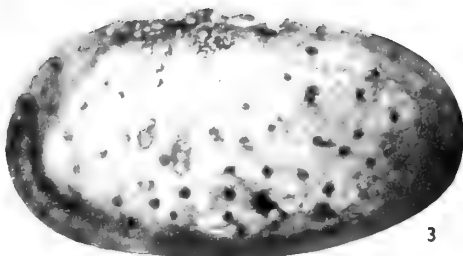
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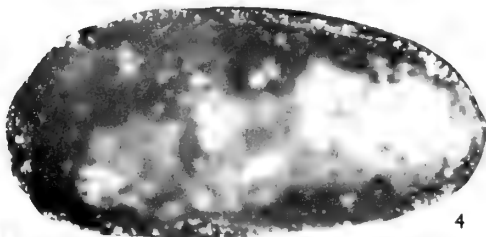
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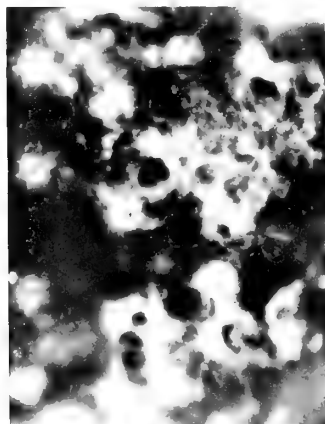
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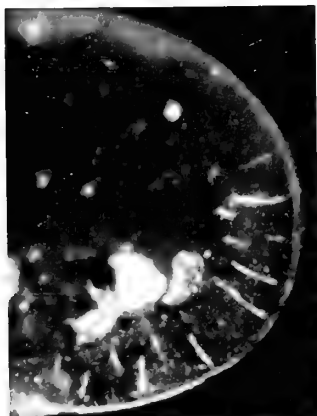
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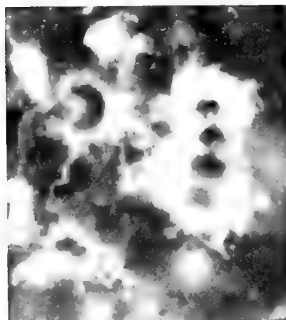
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10



11





PLATE 5

Tetracytheridea punctata gen. et sp. nov. p. 33

FIGS. 1, 2, 6. Right, dorsal and ventral views, female holotype Io. 944.

FIG. 3. Muscle scars, right valve, female paratype Io. 949 × 180.

FIGS. 4, 5, 8. External, internal and dorsal views, right valve, female paratype Io. 946.

FIGS. 7, 10, 11. Dorsal, external and internal views, left valve, female paratype Io. 945.

FIG. 9. Internal view, right valve showing radial pore canals, female paratype Io. 948 × 88.





PLATE 6

Tetracytheridea punctata gen. et sp. nov. p. 33

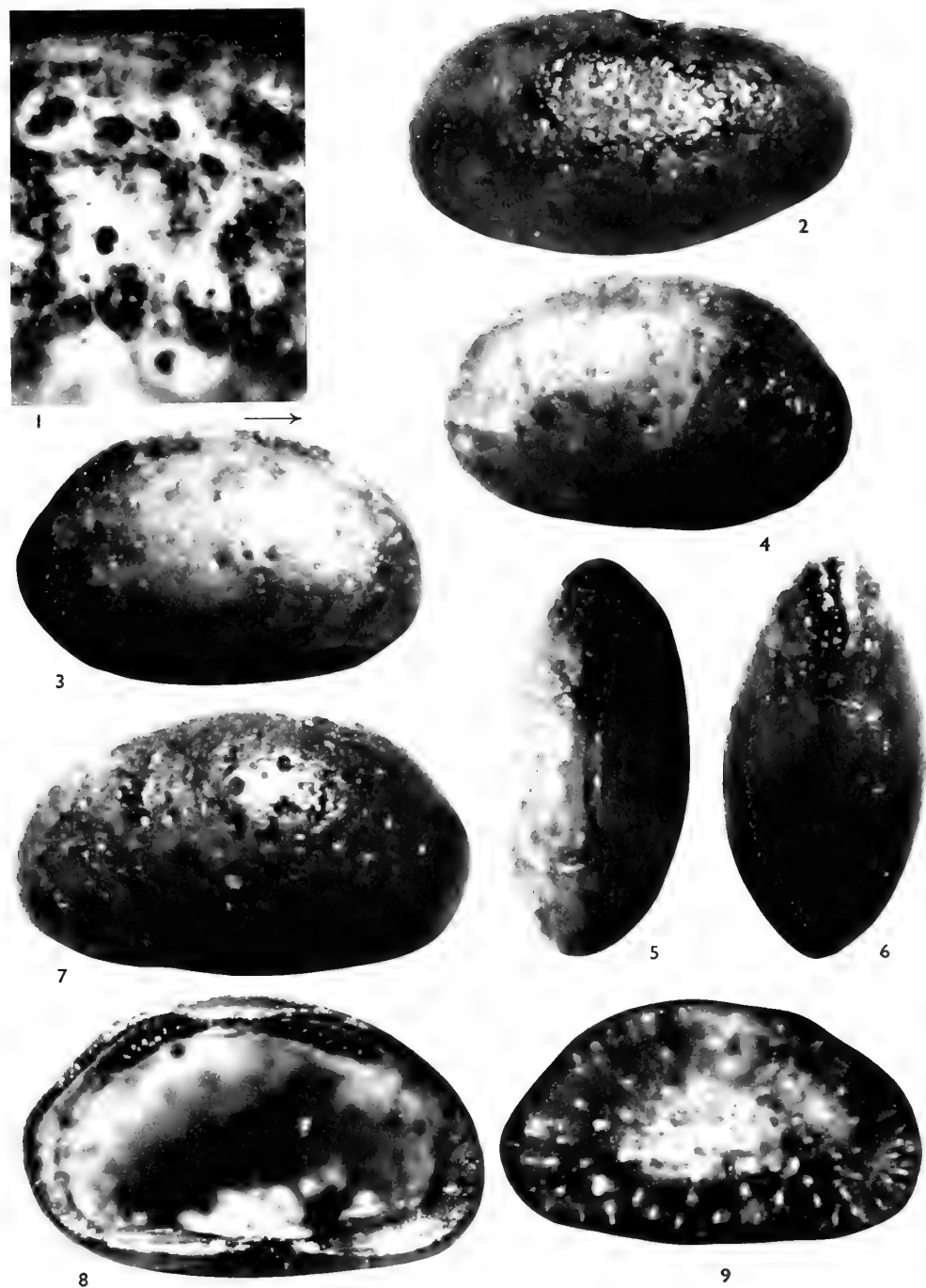
FIGS. 1, 2. Antennal and dorsal muscle scars (Fig. 1 \times 200) and external view, left valve, male paratype Io. 947.

Asciocythere lacunosa sp. nov. p. 34

FIGS. 3-6. Right, left, dorsal and ventral views, holotype Io. 950.

FIGS. 7, 8. External and internal views, left valve, paratype Io. 951.

FIG. 9. External view, right valve, showing muscle scars and pore canals, paratype Io. 952.



TETRACYTHERIDEA, ASCIOCYTHERE



PLATE 7

Asciocythere lacunosa sp. nov. p. 34

FIGS. 1, 2, 4, 6. External and internal views, muscle scars (Fig. 4 \times 220, retouched) and dorsal view, right valve, paratype Io. 952.

FIG. 3. External view, right valve, showing normal and radial pore canals, paratype Io. 953.

FIG. 5. Dorsal view, left valve, paratype Io. 951.

Eocytheridea elongata gen. et sp. nov. p. 35

FIGS. 8, 9, 10. Dorsal, external and internal views, right valve, holotype Io. 954.

FIGS. 7, 11, 12. Dorsal, external and internal views, left valve, paratype Io. 955.

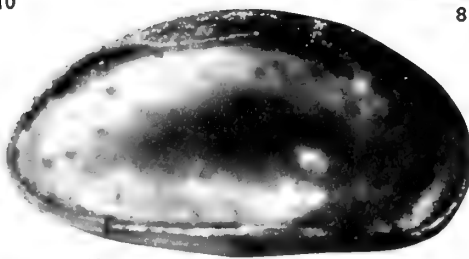
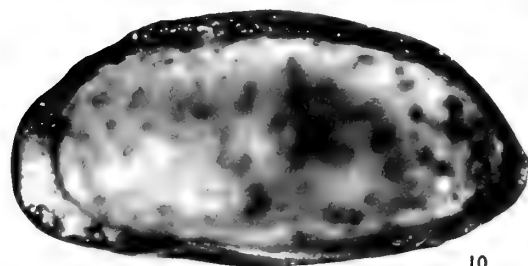
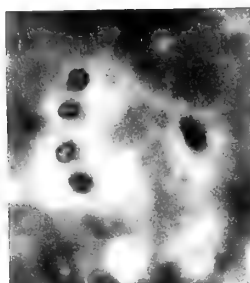
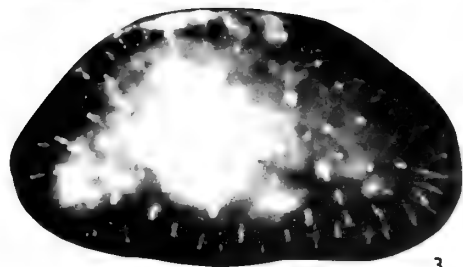
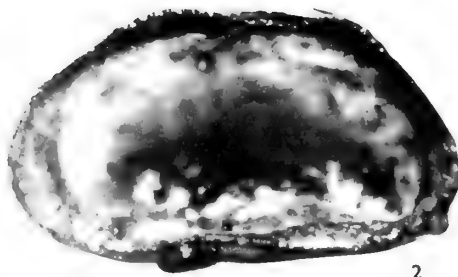




PLATE 8

Eocytheridea elongata gen. et sp. nov. p. 35

FIGS. 1, 2. External view (showing normal and radial pore canals) and internal view (showing radial pore canals), Fig. 2 \times 180. Right valve, paratype Io. 956.

FIG. 3. Internal view, left valve, paratype Io. 959.

FIG. 4. Ventral view, paratype Io. 958.

FIG. 5. Muscle scars (dorsal adductor retouched), right valve, paratype Io. 957 \times 270.

Eocytheridea lacunosa gen. et sp. nov. p. 36

FIGS. 6, 8, 9. Ventral, right and left views, female holotype Io. 960.

FIGS. 7, 10, 11. Dorsal, external and internal views, male paratype Io. 964.

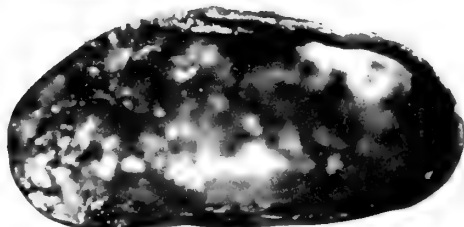
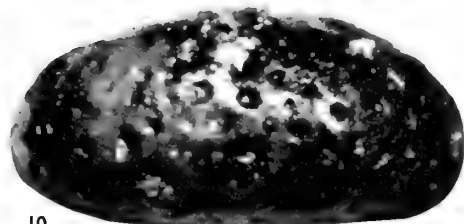
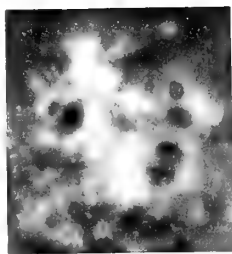
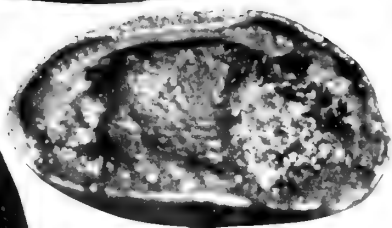
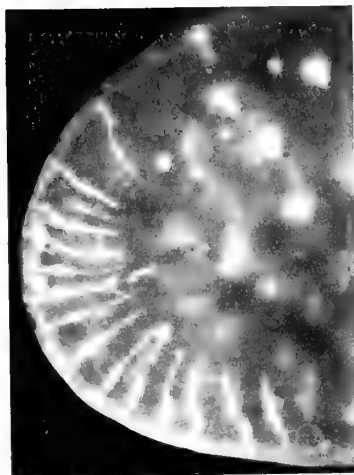
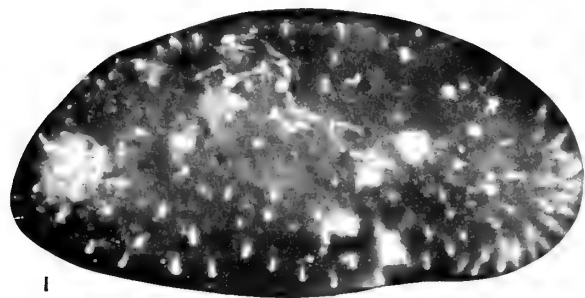




PLATE 9

Eocytheridea lacunosa gen. et sp. nov. p. 36

FIGS. 1-4. Left, right, ventral and dorsal views, male paratype Io. 961.

FIGS. 5, 6. External and internal views, left valve, male paratype Io. 963.

FIGS. 7, 8. External view, showing muscle scars and normal pore canals, and internal view (Fig. 8 $\times 180$), showing radial pore canals, right valve, paratype Io. 962.

Paraschuleridea ornata sp. nov. p. 37

FIGS. 9, 11, 12. Dorsal, internal and external views, left valve, holotype Io. 965.

FIG. 10. Dorsal view, right valve, paratype Io. 966.



PARASCHULERIDEA, PRAESCHULERIDEA





PLATE II

Praeschuleridea ventricosa ventricosa (Plumhoff) p. 39

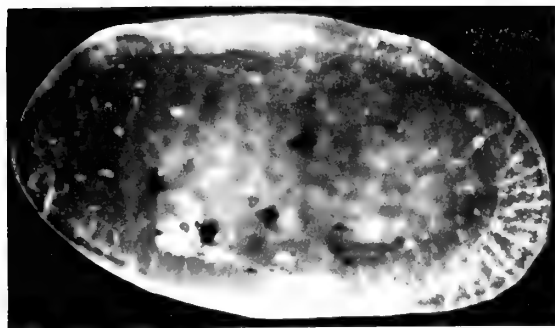
FIG. 1. Internal view showing radial pore canals, left valve, male paratype Io. 980.

FIGS. 2, 4, 5. Right, dorsal and ventral views, female paratype Io. 976.

FIGS. 3, 6. Internal and external views, left valve, female paratype Io. 974.

FIGS. 7, 9. External and internal views, right valve, male paratype Io. 978.

FIG. 8. Internal view, left valve, male paratype Io. 977.



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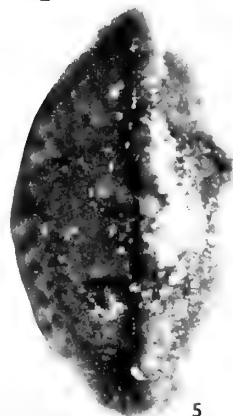
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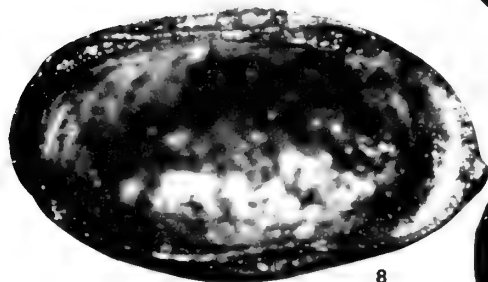
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7



8



9





PLATE 12

Praeschuleridea ventricosa ventricosa (Plumhoff) p. 39

FIGS. 1, 2, 8. External, internal and dorsal views, right valve, female paratype Io. 975.

FIG. 3. Muscle scars, left valve, male paratype Io. 982 × 280.

FIG. 4. Muscle scars, right valve, male paratype Io. 981 × 360.

FIG. 7. Dorsal view, hinge, left valve, female paratype Io. 974.

Cytheropterina comica sp. nov. p. 41

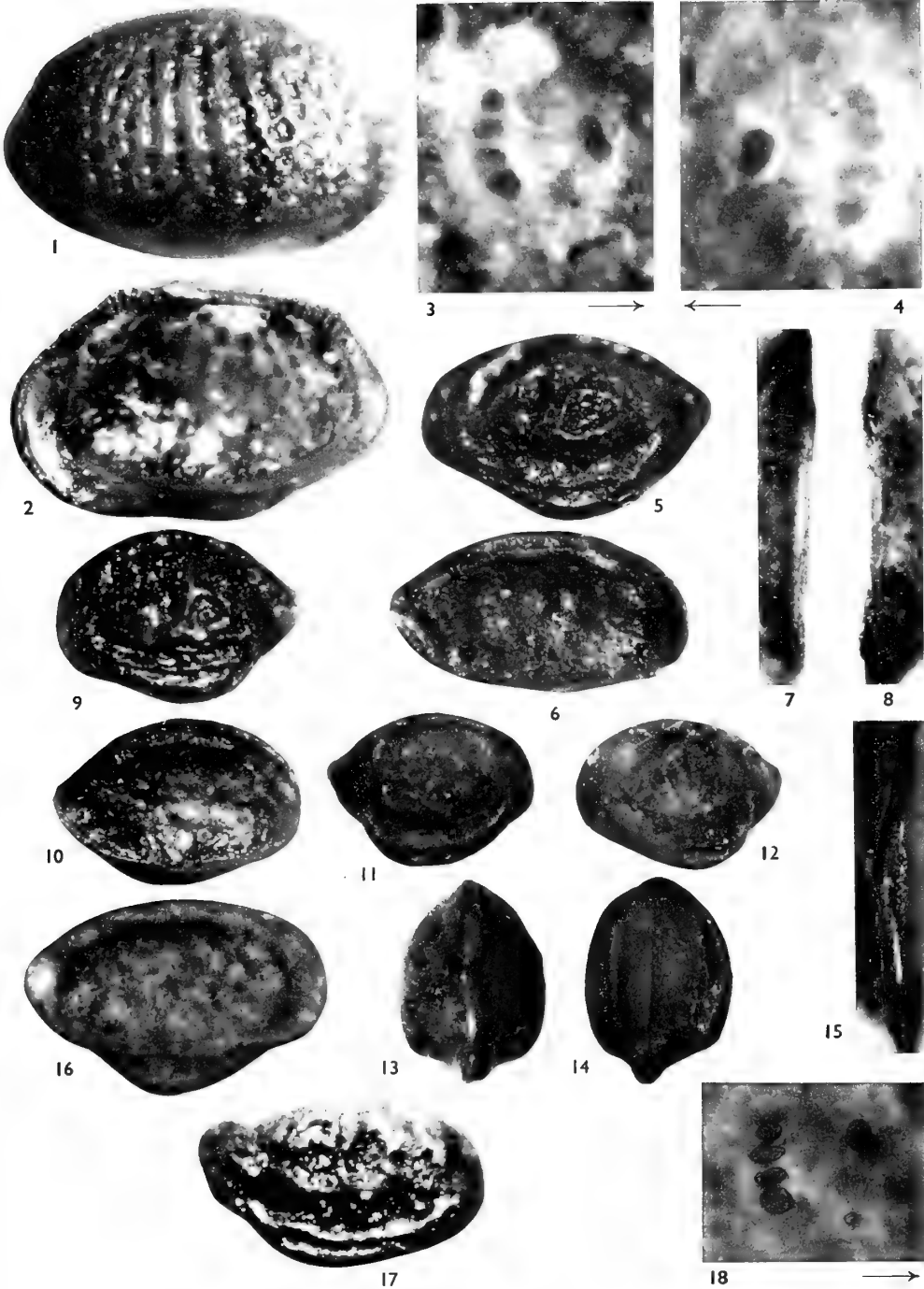
FIGS. 5, 6, 15. External, internal and dorsal views, left valve, male paratype Io. 993.

FIGS. 9, 10. External and internal views, left valve, female holotype Io. 990.

FIGS. 11-14. Right, left, dorsal and ventral views, female paratype Io. 991. Kirton Cementstone Series. Lincoln.

FIGS. 16, 18. Internal view showing muscle scars (Fig. 18 × 340), left valve, male paratype Io. 994.

FIG. 17. External view, right valve, male paratype Io. 996.



PRAESCHULERIDEA, CYTHEROPTERINA





PLATE 13

Cytheropterina gravis sp. nov. P. 42

FIGS. 1, 2, 7. External, internal and dorsal views, left valve, male holotype Io. 998.

FIGS. 3, 6, 8. External, internal (Fig. 6 \times 115) and dorsal views, right valve, female paratype Io. 999.

FIGS. 4, 5. External and internal views, left valve, female paratype Io. 1000.

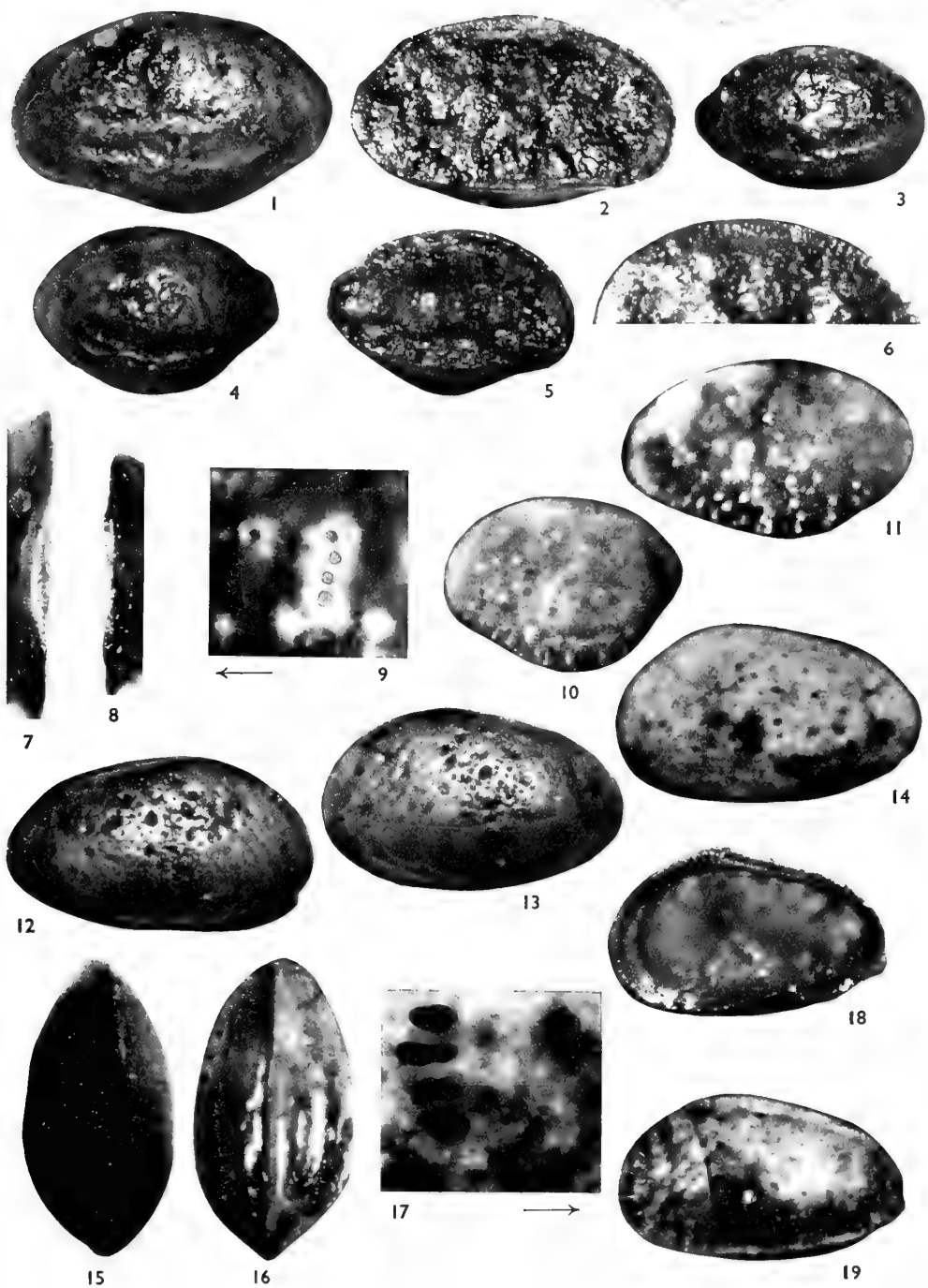
FIGS. 9, 11. Muscle scars (Fig. 9 \times 280) and external view, left valve, male paratype Io. 1002.

FIG. 10. Left valve, external view, to show muscle scars, female paratype Io. 1001.

Kinkelinella ? bajociana sp. nov. P. 44

FIGS. 12-16. Right, left (Fig. 14 in glycerine to show muscle scars and pore canals) dorsal and ventral views, holotype Io. 1008.

FIGS. 17-19. Muscle scars (Fig. 17 \times 319) and internal views showing hinge and radial pore canals, right valve, paratype Io. 1009.



CYTHEROPTERINA, KINKELINELLA?

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THE STILE END BEDS AND DRYGILL
SHALES (ORDOVICIAN) IN THE EAST
AND NORTH OF THE ENGLISH LAKE
DISTRICT

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 9 No. 3

LONDON : 1963

THE STILE END BEDS AND DRYGILL SHALES
(ORDOVICIAN) IN THE EAST AND NORTH OF
THE ENGLISH LAKE DISTRICT

BY
WILLIAM THORNTON DEAN, Ph. D.

Pp. 47-65 ; 5 Plates ; 3 Text-figures

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THE STILE END BEDS AND DRYGILL SHALES (ORDOVICIAN) IN THE EAST AND NORTH OF THE ENGLISH LAKE DISTRICT

By W. T. DEAN

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SYNOPSIS

Previous opinions regarding the stratigraphical position of the Stile End Beds and Drygill Shales are reviewed and revised in the light of recent field-work. Geological maps showing the principal fossil localities are included, and all the significant shelly fossils are discussed and illustrated. One new trilobite species, *Encrinurus kingi*, is described from the Stile End Beds.

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE group of Ordovician strata immediately overlying the Borrowdale Volcanic Series in the main portion of the Lake District forms a narrow, strip-like outcrop running from the Lancashire coast near Millom, north-eastwards to a point near Shap, Westmorland, by way of Coniston, a distance of about thirty-two miles. The name Coniston Limestone Group or Series has generally been applied to these rocks, the nomenclature of which has been reviewed by Mitchell (1956 : 431). Earlier the same author (Mitchell 1925) had established the following detailed succession of Ordovician rocks in the north-eastern part of the outcrop :—

Ashgill Shales	}	up to 400 feet
Applethwaite Beds						
UNCONFORMITY						
Stockdale Rhyolite	0 to 450 feet
Stile End Beds, with conglomeratic base	up to 250 feet
UNCONFORMITY						
Borrowdale Volcanic Series						

There seems to have been a tendency for many geologists to regard the whole of this succession as being of Ashgill age, probably in deference to Marr's assertion (1916 : 38) that the fauna of the Stile End Beds was apparently identical with that

of the Applethwaite Beds. In fact, apart from the trilobites *Phacops* (now *Chasmops*) *marri* (Reed 1894) and *Acidaspis magnospina* (Stubblefield 1928), no shelly faunas have been figured or described from the whole of the succession, and previous faunal lists are so out of date as to be virtually valueless to stratigraphers at the present day. The present detailed investigation of the Stile End Beds has been restricted to the type-area, east of Kentmere, and it shows that these strata belong to the Caradoc Series, though representing only a small part of the classical type-succession as found in south Shropshire and, to a lesser extent, the Cross Fell Inlier, about twelve miles north-east of Shap Fell. In addition to my personal collecting, the late Prof. W. B. R. King generously placed at my disposal his collection, now in the Sedgwick Museum, from the same area.

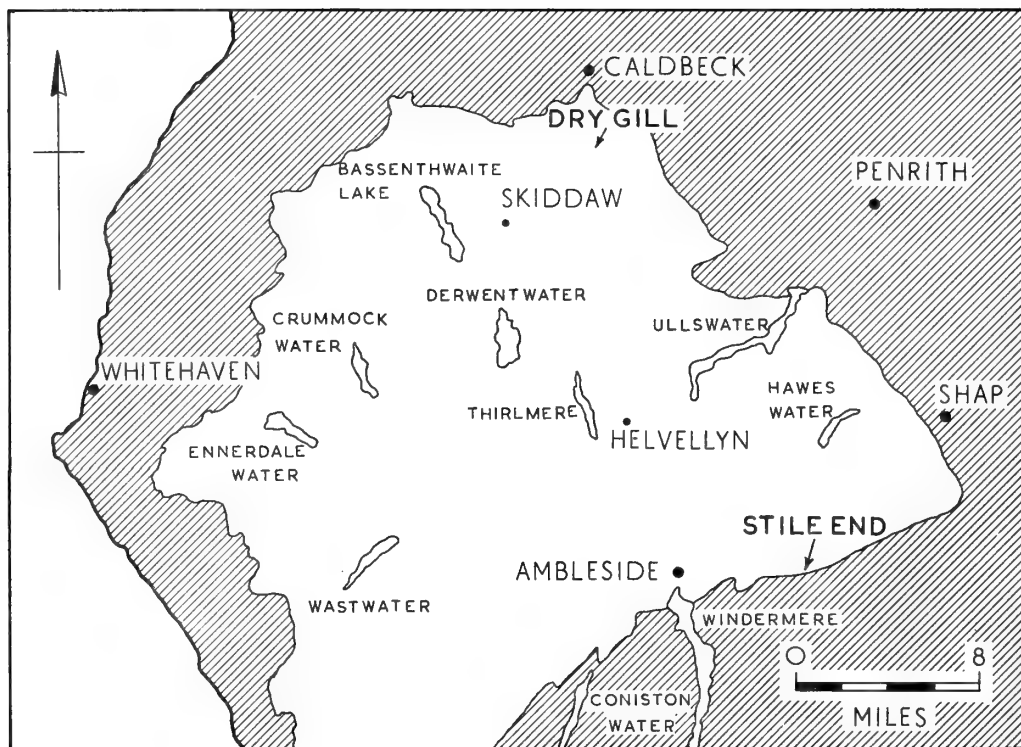


Fig. 1. Sketch-map showing the position of Stile End and Dry Gill in relation to the rest of the Lake District.

The Drygill Shales, known only from their small, isolated outcrop just to the north of Carrock Fell, Cumberland, in the extreme north of the Lake District, have been generally neglected by palaeontologists and stratigraphers. Stubblefield (1939 : 56), noting their Caradoc age, commented on the presence of what he called the *Broeggerolithus* - "*Acaste*" - *Brongniartella* fauna, and remarked on its affinities with those of the Llyn Peninsula, North Wales. However, no fossils have yet been figured from this interesting, but tectonically disturbed, outcrop. During

the present mapping, numerous trilobites and brachiopods have been obtained, and I am much indebted to my wife for her help in collecting, both here and at Stile End. Dr. C. L. Forbes has loaned the specimens, now in the Sedgwick Museum, which were collected by Elles & Wood and listed by them in their paper of 1895. Prof. W. F. Whittard has kindly read and criticised the manuscript and made suggestions for its improvement.

II. THE STILE END BEDS EAST OF KENTMERE

(a) *General account*

The Stile End Beds form a strip-like outcrop varying in breadth from approximately 70 to 150 yards and extending east-north-eastwards from Kentmere towards Shap by way of Long Sleddale (see Text-fig. 2). The strata comprise a conglomeratic horizon of variable thickness passing upwards into dark-grey mudstones, the latter being sometimes strongly cleaved so as to form poor quality slates which were once quarried on a small scale near Stile End farm itself, as was noted by Harkness & Nicholson (1866). They are overlain by the Stockdale or Yarlside Rhyolite, and this is followed in turn by the Applethwaite Beds, of Ashgill age, which overstep the foregoing strata. The Stockdale Rhyolite crops out only in the eastern part of the Lake District, but the Stile End Beds and Applethwaite Beds traverse the Lake District in a roughly south-westerly direction. In the present paper only the Stile End Beds east of Troutbeck are considered; this is not only the type-area for the strata, but is apparently the most fossiliferous part of the outcrop.

The first reference to what are now the Stile End Beds was made by Harkness & Nicholson (1866) when they recorded fossils "near the summit" of the Borrowdale Volcanic Series. Later, Aveline (*in* Aveline & Hughes 1888 : 7) subdivided the Coniston Limestone Series into :

Ashgill Shales

Limestone

Felsite

Calcareous ash with fossils.

Of these, the two lowest are now the Stile End Beds and Stockdale Rhyolite, in ascending order.

Harkness & Nicholson (1877 : 461-2) described a "band of brownish or bluish grey shales . . . separated from the Coniston Limestone by a bed of trap" at what they called "Style-End Grassing". The latter name is not shown on the present-day Ordnance Survey Maps or the Old Series Geological Survey map, and presumably refers to the grass covered area to the east of Stile End Farm. The age and position of the beds were not discussed, but the fauna was said to be of Bala type and the fossils listed included *Calymene blumenbachi* Brongniart, *Orthis vesperilio* Sowerby and *Petraia aequisulcata* M'Coy.

Marr (1892 : 97, 99) used the term Stile End Beds for the basal subdivision of the Coniston Limestone Series near Kentmere, and later (Marr 1916 : 38) he stated that the fauna of these strata seemed identical with that of the Applethwaite Beds—a conclusion now known to be incorrect, as the latter subdivision is of Ashgill age. The

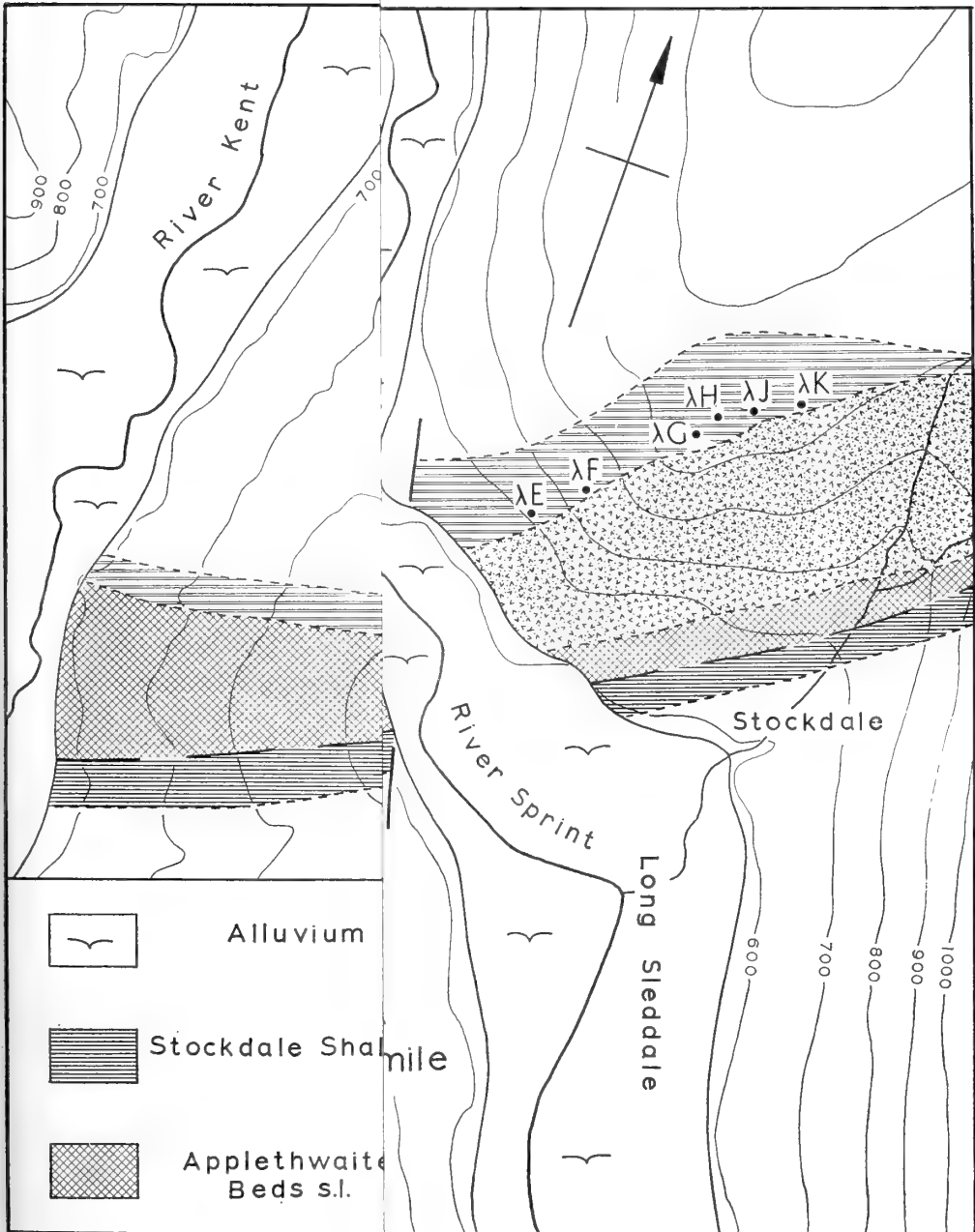
outcrop of the Stile End Beds was depicted by Mitchell (1925) and, together with additional field-mapping by the writer, forms the basis of the locality-map in the present paper. Mitchell also showed the relationship of the overlying Stockdale Rhyolite and the overstep at the base of what he called the Upper Coniston Limestone, now the Appleshwaite Beds. The last-named strata and their basal conglomerate, with the Stile End Beds and Yarlside Rhyolite, had earlier been placed by Marr (1892 : 97 *et seq.*) in the Sleddale Group, but in view of the stratigraphical gaps now known to exist in the higher Ordovician rocks of northern England it seems preferable to allow this term to lapse.

Shelly fossils have now been collected from several localities at various levels through the succession and at points situated along the outcrop east of Kentmere. Trilobites and brachiopods have been obtained from most of the localities and they enable a reasonable correlation to be made with part of the Caradoc succession in south Shropshire. Although no definite limestone bands are developed in the Stile End Beds east of Kentmere, and there is no suggestion of reef-formation, nevertheless both solitary rugose and compound tabulate corals are not uncommon, the latter generally occurring as isolated "sops" within the grey mudstones.

(b) *List of fossiliferous localities*

The following list does not claim to be comprehensive, as unidentifiable and fragmentary shelly fossils have been found at other points along the outcrop, but it comprises all localities which yielded identifiable material during the present field-work. Further collecting is always likely to establish additional localities.

- λA. 1,800 feet at 82° from main building of Stile End Farm.
- λB. Although shown on the map as one locality, in practice three closely-grouped localities were used, as follows :
 - λB1. 2,650 feet at 76°
 - λB2. 2,580 feet at 77°
 - λB3. 2,540 feet at 78½°
 } from main building of Stile End Farm.
- λC. 3,510 feet at 76° from main building of Stile End Farm.
- λD. 3,490 feet at 77° " " " " " "
- λE. 2,000 feet at 325° from Stockdale Bridge, Long Sleddale.
- λF. 2,040 feet at 335° " " " " "
- λG. 2,300 feet at 348° " " " " "
- λH. 2,380 feet at 350° " " " " "
- λJ. 2,400 feet at 354° " " " " "
- λK. 2,480 feet at 0° " " " " "



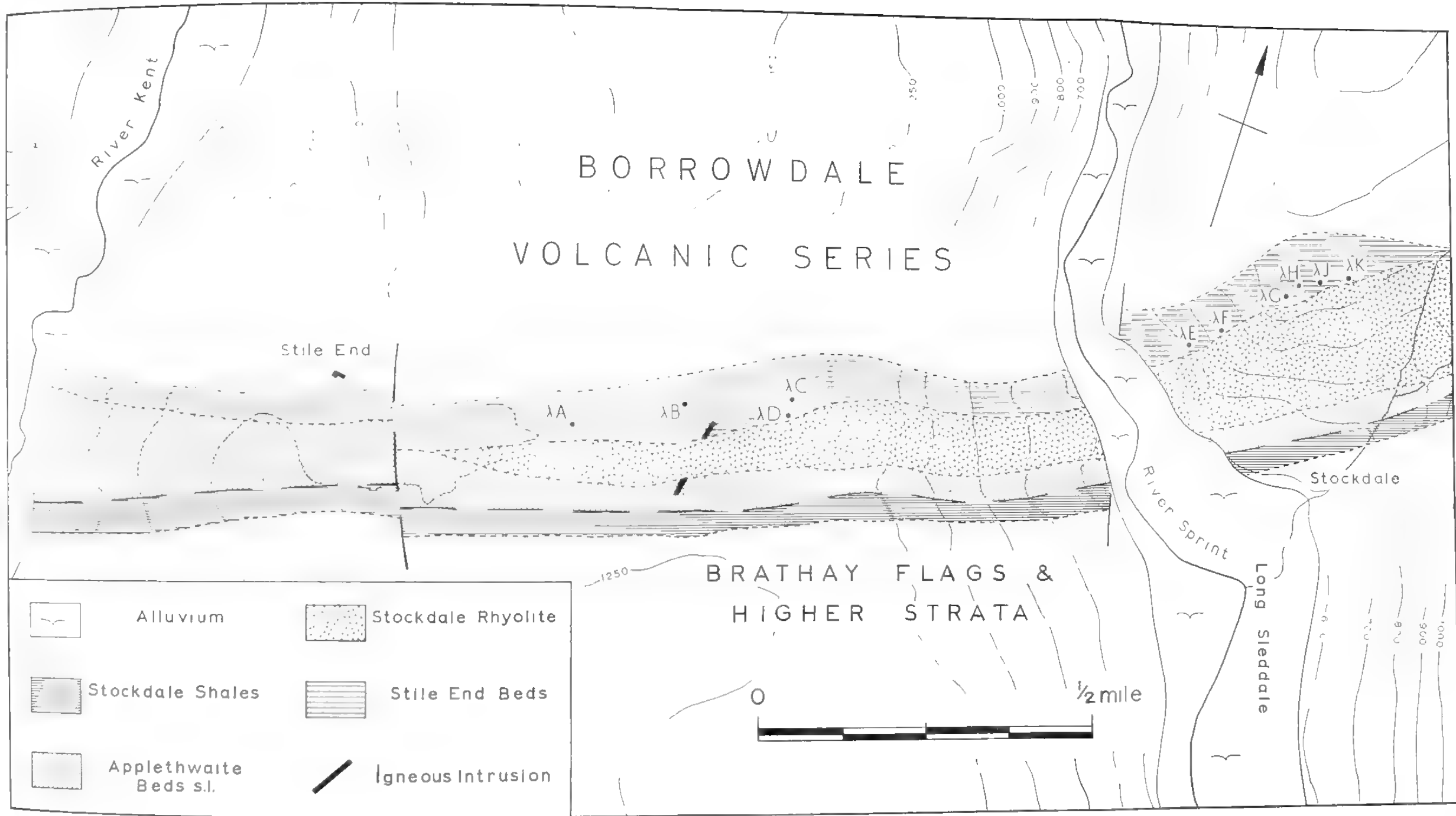


Fig. 2. Map showing fossil localities in the Stile End Beds which are mentioned in the text. Geological boundaries from maps of Mitchell (1925) and the writer.

(c) *Palaeontology*
Class **TRILOBITA**

Family **ENCRINURIDAE** Angelin 1854

Genus **ENCRINURUS** Emmrich 1844

Encrinurus kingi sp. nov.

(Pl. 1, figs. 6, 7, 12 ; Pl. 2, figs. 1, 2, 7)

DIAGNOSIS. Cephalon of characteristic *Encrinurus* form, with coarsely tuberculated surface. Pygidium subtriangular in plan. Axis with at least 25 entire axial rings ; side-lobes with eleven pairs of pleural ribs ending in small free points.

HOLOTYPE. Sedg. Mus. A.51706 (Pl. 2, fig. 1).

PARATYPES. Sedg. Mus. A.51705 (Pl. 1, figs. 6, 7); British Museum (Nat. Hist.), In. 56791 (Pl. 2, fig. 7); In. 56979 (Pl. 1, fig. 12) ; In. 56993 (Pl. 2, fig. 2).

LOCALITY AND HORIZON. All the known specimens are from the Stile End Beds in Long Sleddale, locality 1F.

DESCRIPTION. No complete cranidium has yet been found, and of the fragments available only one shows the glabella. The latter is roughly twice as long as broad, strongly convex both longitudinally and transversely, and expands forwards gently to a short frontal glabellar lobe which overhangs the anterior border. There are three pairs of small glabellar lobes of equal size, separated from one another by smooth, notch-like indentations denoting the glabellar furrows. The occipital furrow is broad (*sag.*) and of moderate, uniform depth. The occipital ring is of about the same length (*sag.*) as each of the glabellar lobes, and is ornamented with five large tubercles. Similar coarse tuberculation covers the surface of the glabella, but is insufficiently well preserved to detect any regular pattern. A fragment of the right fixigena (Pl. 1, fig. 12) is typical of the genus, its surface carrying large tubercles like those of the glabella. The eyes are too poorly preserved to ascertain their exact position.

The species is better known from the pygidium. This is roughly triangular in plan, bluntly pointed posteriorly, almost twice as long as broad, the line of maximum breadth being just behind the anterior margin. The straight-sided axis, with slightly flattened dorsal surface, is fairly narrow, occupies frontally about one quarter of the maximum breadth, whence it narrows backwards uniformly and ends in a blunt point a little in front of the pygidial tip, to which it is connected by a low, post-axial ridge. Axial rings are small and numerous, separated from each other by deeply incised ring furrows which become shallower medially. Each ring is transversely straight for most of its length (*tr.*) but turns backwards slightly at either end. There is apparently no development of axial tubercles, and the axial rings diminish markedly in size towards the axial tip. The holotype pygidium has 25 axial rings, beyond which the terminal piece is apparently smooth. The adaxial half of each side-lobe is approximately horizontal, but the abaxial half is steeply declined beyond a well-defined fulcrum. In addition to the anterior pair of half-pleurae there are

eleven pairs of conspicuous pleural ribs separated by equally broad (*exsag.*) pleural furrows ; both ribs and furrows become progressively less well defined towards the tip of the pygidium. The ribs of the first pair are transversely straight as far as the fulcrum but then flex backwards sharply to the lateral margin where they end in small free points. Subsequent pairs of ribs become progressively straighter but are directed more strongly backwards, so that the final pair runs almost parallel to the axial line. The free points of the posterior ribs are relatively small, as far as can be seen.

DISCUSSION. The species of *Encrinurus* with which the pygidium of the new form may be compared include *E. praecursor* Tripp, *E. multisegmentatus* (Portlock) and *E. trispinosus* Reed. The first of these (Tripp 1954 : 681, pl. 4, figs. 13–25), from the Caradoc Series near Girvan, has a similar number of ribs but more axial rings, up to 32, and many of the ring furrows are obsolete medially. *E. multisegmentatus* (Portlock) from the Killey Bridge Beds of Ireland (perhaps high Caradoc in age) has been redescribed by Tripp (1957 : 61, pl. 12, figs. 1–6), and possesses a greater number of both axial rings (up to 32) and pleural ribs (12 or 13). In addition, some of the ring furrows become obsolete medially, a feature found also in *Encrinurus trispinosus* from the Upper Drummuck Group (Ashgill Series) of Girvan (Reed 1906 : 122–124 ; 1914 : 39).

OTHER TRILOBITES

Several specimens of *Chasmops* (Pl. 1, figs. 1, 2, 5, 10) have been collected from the Stile End Beds at localities λA , $\lambda B1-3$, λC , λD and λG . Most are sheared and distorted, but some show enough diagnostic features to compare them with *Chasmops extensa* (Boeck), a Norwegian species refigured by Størmer (1940 : 138) and recently redescribed and illustrated from south Shropshire (Dean 1961 : 336). In Shropshire the species appears about the middle of the Upper Longvillian Substage and ranges upwards into the lowest zone of the Onnian Stage, but attains its maximum size and abundance in the Actonian. The Stile End specimens are often large, though they never reach the proportions of the largest Shropshire individuals. It is interesting that only three specimens of *Chasmops* cf. *extensa* have been found in what are probably Actonian strata in the Cross Fell Inlier (Dean 1962 : 104), though the general absence of the species there is probably due less to ecological factors than to elimination of the appropriate strata by faulting.

Only one damaged specimen (Pl. 1, figs. 3, 4) of *Calyptaulax* cf. *actonensis* Dean (1961 : 328), a laterally compressed pygidium with abraded axis, has been found. The pleural lobes carry six pairs of pleural furrows, extending from the axial furrows to the inner margin of the doublure, and five or perhaps six pairs of rib furrows, developed across the distal half of each pleural lobe. These figures correspond with those found in the better-preserved type-material from south Shropshire. The tip of the Stile End pygidium is apparently narrower and sharper than that found in Shropshire specimens, but is probably the consequence of mechanical deformation. The new record of *Calyptaulax* is interesting because the genus, although abundant and widespread in the Ashgill Series of both the Anglo-Welsh area and Scotland, is known only in Shropshire from the Actonian and basal Onnian, and at Cross Fell

from the Onnian and Purgillian—that is to say, in these localities it is presumably confined to the uppermost Caradoc Series.

A few specimens probably referable to *Gravicalymene* have been found in the Stile End district. Only one, a cranidium (Pl. 1, fig. 11), is sufficiently well preserved for comparison, and is figured here as *Gravicalymene* cf. *praecox* (Bancroft). This specimen, although slightly compressed laterally, nevertheless shows a glabellar outline and unconstricted axial furrows, as well as part of a thickened anterior border, such as are found in *Gravicalymene praecox*. The latter species was first described by Bancroft (1949 : 308) as *Diacalymene praecox* from the Harnagian Stage of south Shropshire. Since then the species has been placed in *Gravicalymene*, and it has been shown that closely similar trilobites reappeared in the Onnian and, more especially, Actonian Stages of Shropshire (Dean 1963 : 225). The latter form may therefore be contemporaneous with the Stile End specimen.

A single large cranidium of *Atractopyge* (Pl. 2, figs. 3, 5), collected by Professor King from locality λG, is the only example of the genus so far known with certainty from the Stile End district. The material is insufficient for precise identification, but there is a general resemblance to *Atractopyge scabra* (Dean 1962 : 91) from the Onnian and Purgillian Stages of the Cross Fell Inlier, though the frontal glabellar lobe of the latter species is apparently shorter. Further comparison is not possible. The genus had a long, though sporadic, history in the Ordovician of England and Wales, being known from rocks as early as the Llandeilo Series and as late as the Ashgill Series. In south Shropshire, however, only a single specimen, a pygidium, is recorded from the Actonian Stage (Dean 1961 : 318), and may be regarded as approximately contemporaneous with the present cranidium.

Two specimens of *Proetidella*?, a right librigena and an incomplete cranidium (Pl. 1, figs. 8, 9) from λE and λG, are the sole representatives of the Proetidae so far known from the Stile End Beds. The glabella is broadly parabolic in plan with a distinct preglabellar furrow. The preglabellar field and anterior border furrow are well defined, whilst the anterior border forms a low, upturned brim. In some respects the specimen resembles the type-species of *Proetidella*, *P. fearnsidesi* Bancroft (1949 : 304), but the latter form has, in most cases, a less well-defined anterior border furrow, though there is some variation within the species (Dean 1963 : 243). The anterior border of the Stile End specimen somewhat resembles, but is set lower than, that of the uncommon species *Proetidella? marri* (Dean 1962 : 124) from the Lower Longvillian of the Cross Fell Inlier. In south Shropshire, where *Proetidella* probably ranges from the Costonian to the Actonian, fragments of generally similar type have been recorded from the Marshbrookian and Actonian Stages (Dean 1963 : 246) but are insufficiently known for comparison.

OTHER FOSSIL GROUPS

A few indifferently preserved dalmanellids which may be compared with *Cryptothyris paracyclica* (Bancroft) have been found near Stile End at localities λC, λG, and λK. The best preserved specimen, the internal mould of a brachial valve (Pl. 2, fig. 6), is apparently shorter and more convex than the type material, due to mechanical deformation. However, it shows the peripheral zone of sharply

defined ribbing noted by Bancroft in his original description (1928 : 56, pl. 1, figs. 6–9). Even more conspicuous is the area occupied by the adductor muscle impressions, which extends more than half-way from the crurae to the anterior commissure and is divided into two by a longitudinal ridge, with a transverse ridge separating the anterior and posterior adductor impressions, of which the latter are conspicuously the smaller. In south Shropshire *Cryptothyris paracyclica* has been found to be a reliable Actonian index fossil (Dean 1958 : 211, pl. 25, fig. 7), but the genus is uncommon and has not previously been recorded elsewhere. *Nicolella* cf. *actoniae* (J. de C. Sowerby) (Pl. 3, figs. 5, 9) also refers to a common Actonian species in Shropshire.

Sowerbyella is represented by a few specimens (for example Pl. 2, figs. 10, 11) at localities λB1 and λB2. The type-species, *Sowerbyella sericea* (J. de C. Sowerby) from the Upper Longvillian of south Shropshire, has recently been redescribed by Williams (1963 : 446) and bears a general resemblance to the Stile End individuals. However, there is a variety of forms of *Sowerbyella* distributed throughout most of the Caradoc Series of the Anglo-Welsh area, and no detailed comparison is possible with the present distorted material.

The Stile End brachiopods include at least four strophomenid genera. Several fragments of *Leptaena* have been found (see Pl. 3, fig. 8) at localities λB1 and λD and may, perhaps, be compared to *L. salopiensis* Williams (1963 : 477) from the Actonian of south Shropshire. The genus *Hedstroemina* appears in south Shropshire in the Marshbrookian, where it is represented by *H. parva* Bancroft and, more especially, *H. fragilis* Bancroft. In the succeeding Actonian it comprises only *H. robusta* Bancroft, a fairly common species described from the Acton Scott district (Bancroft 1929 : 59, pl. 2, figs. 6, 7). In the vicinity of Stile End a few large specimens have been collected which are close to the last-named species, although, once again, distortion makes specific determination difficult (see Pl. 3, figs. 1–3). *Hedstroemina robusta* has not yet been reported from elsewhere in Britain, but has been recorded from what is probably a slightly earlier horizon in Norway (Spjeldnaes 1957 : 133, pl. 8, fig. 5). The internal mould of a damaged strophomenid ventral valve (Pl. 2, fig. 8) is broadly similar in the form of the crural plates and ornamentation to that of *Strophomena grandis* (J. de C. Sowerby), though the proportions have been altered by deformation. In Shropshire the species ranges from the Upper Longvillian into the Actonian. Another ventral valve (Pl. 2, fig. 9) resembles that of *Rafinesquina*, but lacks evidence of internal structures.

Platystrophia is represented by two internal moulds of pedicle valves (Pl. 3, figs. 4, 7) from locality λG. *Platystrophia* has a long vertical range in the Anglo-Welsh area, and the Stile End specimens cannot satisfactorily be assigned to any known species. The genus is rare in south Shropshire, but has been recorded from the Actonian (Dean 1958 : 223).

The triplesiid *Bicuspina* was erected by Havlíček (1950 : 18) on the basis of the Bohemian *Orthisina cava* Barrande 1848 and said to include also the Anglo-Welsh Caradoc species generally listed as *Triplesia* or *Cliftonia spiriferoides* (M'Coy) (for illustrations see Davidson 1871 : 275, pl. 37, figs. 3–7). One specimen of a brachial

valve (Pl. 3, fig. 10) from locality λG near Stile End shows a pattern of adductor muscle impressions closely similar to those of *B. spiriferoides* but is otherwise too poorly preserved for comparison. The same form occurs also at λB_1 and λD . In Shropshire and Wales all the recorded occurrences of *Bicuspina* are from earlier subdivisions of the Caradoc, particularly the Lower Longvillian.

None of the other brachiopods has proved stratigraphically useful, and a few indeterminate valves possibly referable to *Dolerorthis* (for example Pl. 3, fig. 6) belong to a long-ranging and inadequately-known group.

Occasional remains of gastropods in the Stile End Beds have proved inconclusive with regard to the age of the rocks. The best preserved (Pl. 2, fig. 4) is a distorted internal mould of *Cyrtolites* cf. *nodosus* (Salter), a species which has a long vertical range in south Shropshire, from the Soudleyan to the Actonian (Dean 1958 : 220–223).

Corals, both solitary and compound, are not uncommon in the Stile End Beds, particularly in the outcrops of Long Sleddale. They were mentioned briefly by Hill (1951 : 20–21) who stated that they originated from the “Coniston Limestone” *sensu lato*, and noted that it was difficult to tell which came from Marr’s Caradoc or Ashgill Series, though they derived in the main from the “Sleddale Group” (see earlier). She recorded *Syringophyllum* (now *Sarcinula*) *organum* (Linné), *Streptelasma aequisulcatum* (M’Coy) and *Halysites* as being abundant, a fauna resembling that of the Robeston Wathen Limestone of South Wales, and, in addition, a “wide-tubed *Propora*” was noted.

The following coral genera have recently been found : *Streptelasma* (λA , λB_2 , λB_3 , J), *Halysites* (λB_3 , λG), *Lichenaria*? (λJ) and *Propora* (λC , λG , λH , λK). The detailed distribution of the British Ordovician corals is poorly known at the present time, but in view of the Actonian age of the Stile End Beds, it would not be surprising to find that the affinities of the contained corals do, in fact, lie with those of the Robeston Wathen Limestone, which occupies a stratigraphical position high in the Caradoc Series of South Wales, though its exact zonal level in the shelly facies is still obscure.

III. THE DRYGILL SHALES

(a) General Account

The Drygill Shales (see Text-fig. 3) form an irregularly lenticular outcrop, about three-quarters of a mile by one-sixth of a mile in size, with long axis running east-west. To the north they are faulted against the Borrowdale Volcanic Series, and to the south against granophyres of the Carrock Fell Igneous Complex, whilst to both east and west they are interdigitated with dyke-like extensions from the Harestones Felsite, itself also a constituent of the Carrock Fell Complex.

The strata were first noted by Ward (1876 : 17, 24) who briefly referred them to the Skiddaw Slates and considered them to represent a transitional series between those beds and the Borrowdale Volcanic Series. Their true significance was first appreciated by Nicholson & Marr (1887) who gave them the name by which they are generally known. These authors showed, by means of a small sketch-map, the

general distribution of the outcrop but left its outline obscure and did not attempt to show the relationships with the surrounding rocks, though they indicated a large expanse of volcanic rocks belonging to the Eycott Series of the Borrowdale Volcanic Series to the north, and a more complex group of igneous rocks in the neighbourhood of Carrock Fell to the south. They listed the following fossils: *Ampyx rostratus* Sars, *Calymene cambrensis* Salter, *Lichas laciniatus* Wahlenberg?, *Stygina munchisoniae* Murchison, *Trinucleus favus* Salter, *Beyrichia complicata* Salter, *Leptaena sericea* Sowerby, *Obolella*? and *Orthis testudinaria* Dalman. Nicholson & Marr believed that the Drygill Shales were younger than the Upper Skiddaw Slates and older than what they called the "Coniston Limestone proper". Although they noted that the fauna agreed best with that of the Dufton Shales of Cross Fell Inlier, they concluded that the shales were lithologically and faunistically distinct from any strata above the Borrowdale Volcanic Series and so probably belonged to the Volcanic Series itself.

In another, later, paper Marr (1892) modified the above view and suggested that the Drygill Shales had probably a greater affinity with the Coniston Limestone. Subsequently, he instigated the reinvestigation of the Drygill faunas by Elles & Wood who later (1895) largely substantiated Marr's modified views and gave long faunal lists, though they pointed out the deformed nature of the specimens constituting the fauna. Their material has been re-examined and the new determinations of the more useful specimens, comprising trilobites, brachiopods and ostracods, are listed below. The numbers refer to the collections of the Sedgwick Museum, but in some cases no specimen has been found.

Specimen	Old identification	New identification
A.40124-25	<i>Ampyx rostratus</i> Sars	<i>Lonchodomas</i> sp.
—	<i>Ampyx tetragonus</i>	No specimen available
A.40146	<i>Ampyx tumidus</i>	<i>Lonchodomas</i> sp.
A.40163-65	<i>Stygina munchisoniae</i>	gen. et sp. indet.
—	<i>Trinucleus seticornis</i>	} No specimens available
—	<i>Trinucleus concentricus</i>	
—	<i>Trinucleus</i> sp. (allied to <i>affinis</i>)	
—	<i>Phacops</i> (<i>Pterygometopus</i>) <i>alifrons</i> ? M'Coy	
A.40143-44	<i>Phacops</i> (<i>Acaste</i>) <i>appendiculatus</i>	<i>Kloucekia apiculata</i> (M'Coy)
A.40145	<i>Phacops</i> sp.	<i>Kloucekia apiculata</i> (M'Coy)
A.40141-42	<i>Dindymene ornata</i> Linnarsson	<i>Lonchodomas</i> sp.
A.40133-40	{ <i>Calymene blumenbachi</i> <i>Calymene senaria</i> <i>Calymene cambrensis</i> }	} <i>Flexicalymene</i> cf. <i>caractaci</i> (Salter)
—	<i>Lichas laciniatus</i>	
A.40161-62	<i>Beyrichia complicata</i>	No specimen available
—	<i>Obolella</i> ? sp.	<i>Tallinnella</i> sp.
A.40079-81	<i>Plectambonites sericea</i>	No specimen available
—	{ <i>Plectambonites transversalis</i> <i>Plectambonites quinquecostata</i> }	} <i>Sowerbyella</i> sp.
A.40082-87	<i>Orthis testudinaria</i>	
A.40088-89	<i>Orthis elegantula</i>	<i>Dalmanella</i> (s.l.) sp.
A.40090-91	<i>Lingula ovata</i>	<i>Lingulella</i> ? sp.

Elles & Wood (1895) followed Nicholson & Marr (1887) in assuming that the

rocks, which dip generally south or south-south-west, formed a uniform succession which could be followed downwards by means of a roughly south-westerly traverse along the southern fork of Dry Gill itself. The succession obtained was as follows, in descending order :

1. Drab-coloured shales, unfossiliferous
2. Blue-grey shales, weathering white
3. Dark blue-grey or black mudstones
4. Volcanic rocks
5. Dark fossiliferous mudstones with trilobites and brachiopods.

On the basis of the faunas they divided the strata into two parts, an Upper Group, characterized by an abundance of *Trinucleus*, and a Lower Group with an abundance of *Ampyx* and *Orthis testudinaria*, though they admitted that such a subdivision might be of only local application. Although Elles & Wood considered the beds to be related to the Dufton Shales and the Sleddale Beds (= Stile End Beds + Yarlside Rhyolite + Applethwaite Beds) their faunal lists included certain forms, such as *Trinucleus seticornis* and *Dindymene ornata*, which, as pointed out later by Marr (1916 : 42), suggested the existence of Ashgill strata. As noted elsewhere in this paper, such a view is not now acceptable.

Since 1916 the Drygill Shales have attracted little attention, and none of the fossils has ever been figured. Hollingworth (1938) showed the general relationships of their outcrop, and described briefly the alteration of the shales by igneous intrusions and mineralizing solutions. He also (p. 209) gave a map of the area, showing the elongated ovoid outcrop of the Drygill Shales interfingered at either end with the Harestones Felsite, and this was later elaborated slightly in the Geological Survey's Regional Handbook for Northern England (*in* Eastwood 1946, fig. 12). Stubblefield (1939 : 56), in discussing what he called the "*Broeggerolithus* - "*Acaste*" - *Brongniartella*" fauna in the Caradoc Series of England and Wales, stated that it was found in an argillaceous facies in both the Pwllheli Mudstones and the Drygill Shales, and linked the latter with the Dufton Shales. Existing knowledge of the Drygill Shales has more recently been briefly reviewed by Mitchell (1956 : 434) who suggests that the beds may rest unconformably on the Borrowdale Volcanics and Skiddaw Slates, and also that the Coniston Limestone Group (used by him in a broad sense) may have extended originally over the whole of the central Lake District. This view now requires modification, and is discussed later.

Basically the rocks are dark-grey mudstones which, as noted by Marr (1916 : 42), bear a marked lithological resemblance to the Dufton Shales of the Cross Fell Inlier. However, they have been much disturbed tectonically and although there appears to be a general dip just west of south, accurate dip readings were found to be unobtainable or of little use so that estimates of thickness are unreliable.

The greater part of the outcrop comprises what appear to be whitish-grey shales, but this appearance results from a combination of cleavage and alteration by the intrusion of the adjacent Harestones Felsite. Hollingworth (1938 : 214) has noted the possible kaolinisation of the so-called "shales" by the felsite, and the latter forms a substantial outcrop both to the east and to the west of that of the Drygill

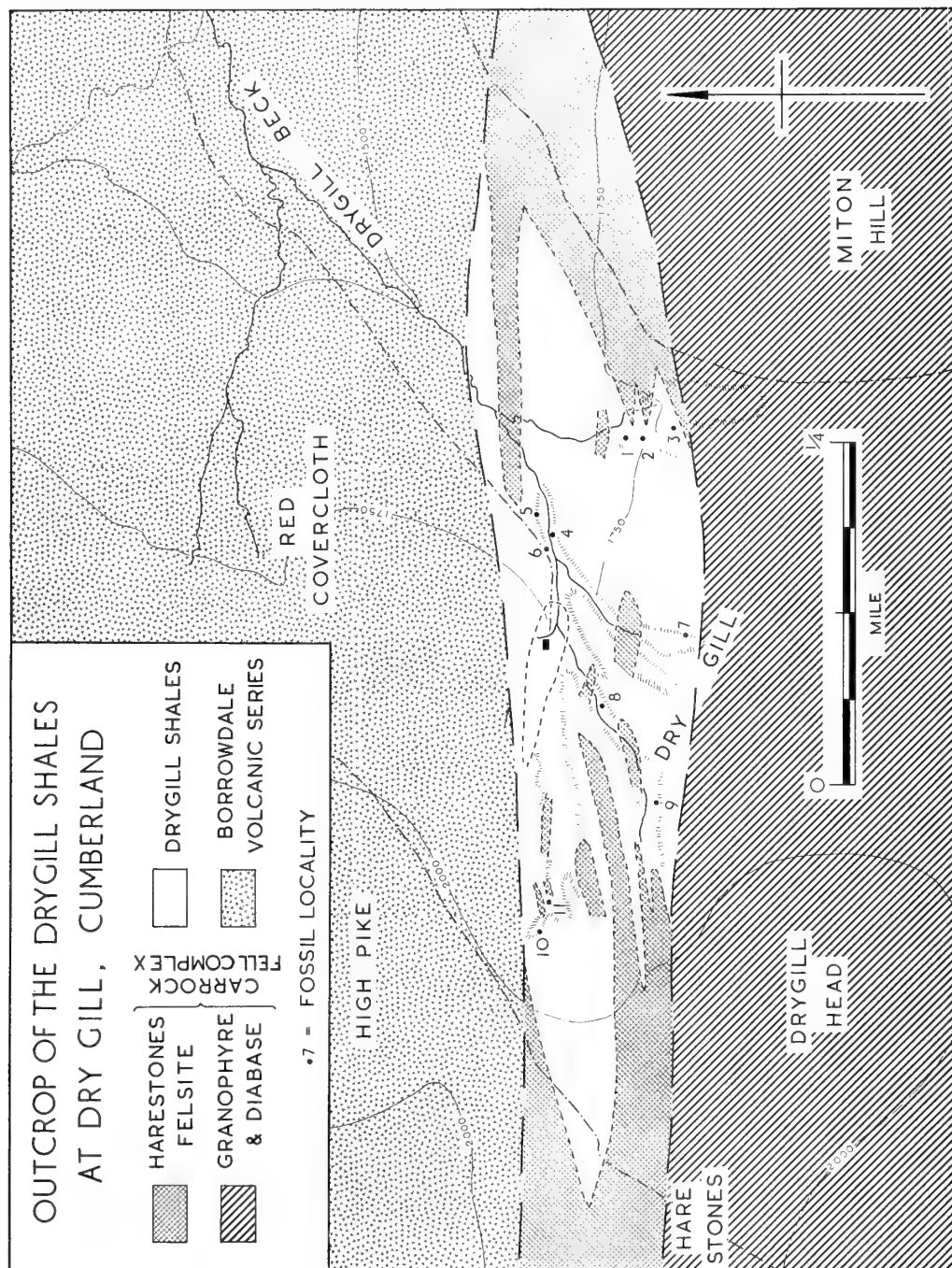


Fig. 3

Shales. The junction of the two is, on the whole, irregularly dentate with occasional dyke-like extensions of the felsite interdigitating with the Caradoc strata and sometimes running for a considerable distance approximately along the strike. No lithological subdivision of the rocks has proved practicable.

(b) *Palaeontology*

Fossils have been found throughout most of the thickness of strata, but the fauna is sporadic, though sometimes apparently occurring in thin bands, as shown by the presence of several specimens on certain slabs of rock. The majority of the fossils are trinucleid trilobites which, as far as the generally poor preservation permits, appear to belong to one species, namely *Broeggerolithus nicholsoni* (Reed) (see Pl. 5, figs. 1, 2, 5, 8, 9, 11). Virtually all the specimens have undergone distortion to a greater or lesser degree and in different directions, so that at first sight there appear to be several different types of cephalae. This obviously led to the misinterpretation of these trilobites by Elles & Wood (1895), and their record of *Trinucleus seticornis* Hisinger sp. (the type species of *Tretaspis*), as well as *Dindymene ornata* Linnarsson, led to an erroneous assumption that Ashgill strata existed at Dry Gill. The occurrence of *Broeggerolithus nicholsoni* through most of the succession suggests that only strata belonging to the Longvillian Stage of the Caradoc Series are present. This species was first described, as *Trinucleus nicholsoni* Reed, from the Alston Road, near Melmerby, in the Cross Fell Inlier. More recently it has been redescribed (Dean 1962 : 79) and shown to occur in what are now called the Melmerby Beds, of Upper and, probably, Lower Longvillian ages. *B. nicholsoni* occurs also in the Pwllheli and Llanbedrog district of North Wales, as well as in the Lower Longvillian of south Shropshire (Dean 1963a : 4, 11), but its distribution is somewhat anomalous as it is almost unknown from the main part of the Cross Fell Inlier.

The attempt made by Elles & Wood (1895 : 248) to subdivide the succession into two parts, an upper with an "abundance of *Trinucleus*", and a lower with abundant "*Amphyx*, *Stygina Murchisoniae* and *Orthis testudinaria*" has not been found practicable. During the present work only a doubtful trace of an indeterminate *Lonchodomas* was seen at Locality 6, but Elles & Wood's collection at the Sedgwick Museum includes a few specimens of the genus, some of them on the same slab of rock. All are distorted, and specific identification is unsafe in view of the state of preservation (see Pl. 4, figs. 3, 10-12). In the Cross Fell Inlier, *Lonchodomas* has been found in only two parts of the Caradoc succession, namely the Upper Longvillian and, higher, in the Onnian and Pusgillian Stages. The specimens from the higher horizon belong to *Lonchodomas pennatus* (La Touche) and have been found almost always in association with such distinctive genera as *Onnia*, *Tretaspis* and *Onnicalymene*, but none of these has yet been found at Dry Gill. Consequently, it seems that the species present may more likely prove to be allied to one such as *Lonchodomas swindalensis* Dean (1962 : 72) from the Upper Longvillian of Cross Fell, though it must be emphasized that specific identification seems unwise with the available material. *Dindymene ornata* as recorded by Elles & Wood (A. 4014-2 in the Sedgwick Museum) probably belongs to the same form of *Lonchodomas*, and

one specimen is figured here (Pl. 4, fig. 6).

All the calymenids examined from Dry Gill have proved to belong to *Flexicalymene* sensu stricto, allied to *F. caractaci* (Salter), though comparison is difficult using such distorted material (Pl. 4, figs. 5, 9). This species-group ranges through the Upper Longvillian and Marshbrookian Stages in south Shropshire, whilst at Cross Fell it is seen in the Lower and Upper Longvillian of the Melmerby district (Dean 1962 : 114).

One cranidium of *Primaspis* has recently been collected by Mr. D. Sealy from Locality 1, and represents the only odontopleurid yet known from the Drygill Shales. The specimen is figured here (Pl. 4, fig. 4) and compared with *P. semievoluta* (Reed), again a trilobite known only from the Longvillian (probably Lower Longvillian) of Melmerby (Dean 1962 : 122).

A few dalmanitid trilobites were found at localities 2 and 11. Although often distorted (see Pl. 5, figs. 4, 7), all appear to belong to *Kloucekia apiculata* (M'Coy), a species which, as far as is known, is a reliable indicator of the Longvillian Stage, at which horizon it is widespread throughout Wales and the Welsh Borders.

Among the generically determinable trilobites found at Dry Gill are two different forms of the homalonotid *Brongniartella*. One of these is the small species *Brongniartella minor* (Salter) (= *B. parva* Harper), recently redescribed (Dean 1961 : 351) and recorded only from the Lower Longvillian of England and Wales. The other, larger species of *Brongniartella* (Pl. 4, fig. 8) has a longer, scoop-like preglabellar field, a convex (as opposed to a transversely straight) anterior border, and a glabellar outline which narrows slightly in front of its mid-point. It is distinct from *B. minor* and may be compared with *Brongniartella bisulcata* (M'Coy), a species ranging from the Upper Longvillian to the Marshbrookian (Dean 1961 : 346) and found in Shropshire and at Cross Fell. The record of *B. minor* at localities 2, 4 and 6 suggests that Lower Longvillian strata occur in the north and eastern part of the Drygill Shales, whilst *B. cf. bisulcata* at locality 9 is suggestive of possibly Upper Longvillian beds to the south-west.

The pygidia listed by Elles & Wood (1895) as *Stygina murchisoniae* Salter are figured here (Pl. 4, figs. 2, 7). Both have undergone lateral compression and are generically undeterminable, though possibly belonging to the Illaenidae or Raphiophoridae.

Of the other fossils of the Drygill Shales, the few dalmanellid brachiopods found have proved inconclusive owing to their poor preservation. They are broadly referable to *Dalmanella* or *Onniella*, but no undistorted internal moulds have been obtained. The single inarticulate brachiopod listed by Elles & Wood as *Lingula ovata* M'Coy is too distorted for certain identification, but probably belongs to *Lingulella*, the genus to which *L. ovata* may, perhaps, be assigned. M'Coy's species (M'Coy in Sedgwick & M'Coy, 1851 : 254, pl. 1.L, fig. 6) was originally described as occurring in the "*Lingula* slates" of Penmorfa and Festiniog, North Wales, as well as the "Coniston Limestone" of Coniston, and, doubtfully, the "Bala schists" of Bryn Melyn, near Bala.

Other brachiopods broadly referable to *Chonetoides* have been collected from localities 1, 3, 5 and 7, and one of the best preserved is figured (Pl. 4, fig. 1).

The remaining fauna includes a few indeterminate gastropods, some machaeridian plates belonging to *Plumulites*, and occasional ostracods which can be broadly assigned to *Tallinnella* Öpik. None of these has proved of stratal significance, and all belong to long-ranging fossil groups.

IV. CORRELATION OF THE CARADOC SERIES IN THE LAKE DISTRICT AND NEIGHBOURING AREAS

Although the faunas of the Stile End Beds have yet to be investigated along the remaining outcrop of the so-called "Coniston Limestone", it is now possible to give at least a broad outline of Caradoc correlation in north-western England. The earliest Caradoc strata there belong to the Longvillian Stage, probably the lower portion of that subdivision. In the south of the Cross Fell Inlier they comprise the distinctive *Corona* Beds of Roman Fell, containing a fauna of mainly inarticulate brachiopods, bivalves and gastropods, with occasional articulate brachiopods and large homalonotid trilobites of the genus *Brongniartella*. At the northern end of the inlier, some fourteen miles away, the corresponding strata comprise blocky, grey-green mudstones with a fauna consisting predominantly of trinucleids belonging to a single species, *Broeggerolithus nicholsoni* (Reed), accompanied by small numbers of other trilobites (*Brongniartella*, *Conolichas*, *Primaspis*) with some brachiopods, mainly small dalmanellids and plectambonitids. These Melmerby Beds would appear to represent an ecological variation distinct from that at Roman Fell, although it seems unlikely that the two were entirely discrete as there is a suggestion of overlap in the vicinity of Dufton, where rare specimens of *B. nicholsoni* have been found with Lower Longvillian brachiopods in dark mudstones. The faunas at Dry Gill indicate that the succession may largely be correlated, first, with the Melmerby Beds, since both contain abundant *Broeggerolithus nicholsoni* and, secondly, with the mudstone succession in the Llyn Peninsula of North Wales, for example the Llanbedrog Mudstones, where the beds contain additional faunal elements of essentially North Welsh type such as *Chasmops* and *Platylichas*, which are unknown from Shropshire and Cross Fell prior to the Upper Longvillian or even later stages. At Dry Gill, as at Cross Fell, owing to the lack of suitable exposures, there is no definite evidence that the base of the Lower Longvillian lies unconformably on the underlying Borrowdale Volcanic Series, but the existence of such an unconformity can hardly be doubted, and indicates a marine transgression in the lower part of the *Dicranograptus clingani* Zone. This may, perhaps, have been a continuation of the earlier, well-known *Nemagraptus gracilis* Transgression, which is now known to have persisted through at least part of the succeeding *Diplograptus multidens* Zone in some areas of the Welsh Borders. On the other hand it might be equated with the instability indicated in parts of south Shropshire during the deposition of the Lower Longvillian rocks, and apparently quite distinct from the *N. gracilis* Transgression.

The Actonian and Onnian Stages of south Shropshire contain faunal elements of Scandinavian type which are unknown from lower strata in the area (Dean 1958 : 229), and the Actonian marks the beginning of a period when faunal regions which hitherto were discrete now became linked. This hypothesis has been supported

in the Cross Fell Inlier, and it has been concluded that these phenomena can be related to the widespread marine transgression, occurring in the late *Dicranograptus clingani* Zone and probably also the *Pleurograptus linearis* Zone, represented by black shales and muds, occasionally graptolitic, known in some areas as the Nod Glas and found over much of Wales (Dean 1959 : 222-223). The Actonian age now established for the Stile End Beds and their basal, marginal conglomerates fills a gap in the stratigraphy of northern England, and suggests a northern geographical limit for the Nod Glas Transgression in the Lake District. Prior to the transgression the Stile End area appears not to have undergone submergence, and there is no suggestion of Lower and Upper Longvillian deposits such as occur at Dry Gill and Cross Fell. Conversely, there is no reliable evidence for the Nod Glas Transgression at Dry Gill, and the margin of the sea must have been twenty miles farther south, in the Stile End area.

Now that the Stile End Beds are known to be Actonian in age, the possible age limits of the Stockdale or Yarlside Rhyolite can be narrowed down to the late Caradoc (Onnian and Pusgillian Stages) or very early Ashgill Series. In view of the fact that Whittington (1950 : 41) has recorded *Diacalymene* from the Applethwaite Beds of Applethwaite Common, two and a half miles west of Stile End, and suggested that the strata are of Lower Ashgill age, the Caradoc age of the Rhyolite seems the more likely. Over most of the Anglo-Welsh area the highest Caradoc beds are either absent or represented by mudstones and shales, and there is no known igneous rock comparable to the Yarlside Rhyolite.

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EXPLANATION OF PLATES

Most of the figured specimens are in the British Museum (Natural History) and their numbers bear the prefixes In., BB. and PG., denoting respectively the trilobites, brachiopods and gastropods. Certain other specimens are in the Sedgwick Museum, Cambridge, and their numbers are prefixed A. Specimens whitened with ammonium chloride before photographing. Photographs by the writer.

PLATE 1

Chasmops cf. *extensa* (Boeck) p. 54

FIG. 1. Internal mould of distorted cephalon. In. 56776. $\times 1.5$. Locality λA .

FIG. 2. Internal mould of pygidium. In. 56978. $\times 1.5$. Locality λG .

FIG. 5. Internal mould of fragmentary pygidium. In. 56803. $\times 1.5$. Locality $\lambda B2$.

FIG. 10. Internal mould of undistorted pygidium. In. 56798. $\times 0.75$. Locality λG .

Calyptaulax cf. *actonensis* Dean p. 54

FIGS. 3, 4. Lateral and dorsal views of internal mould of partly crushed pygidium. In. 56802. $\times 2$. Locality $\lambda B2$.

Encrinurus kingi sp. nov. p. 53

FIGS. 6, 7. Dorsal and lateral views of internal mould of incomplete cranidium. Paratype, SM., A. 51705. $\times 2$. Locality λF .

FIG. 12. Internal mould of fragmentary right fixigena. Paratype, In. 56979. $\times 2$. Locality λF .

Gravicalymene cf. *praecox* (Bancroft) p. 55

FIG. 11. Internal mould of almost complete, damaged cranidium. In. 56786. $\times 3.5$. Locality λE .

Proetidella? sp. indet. p. 55

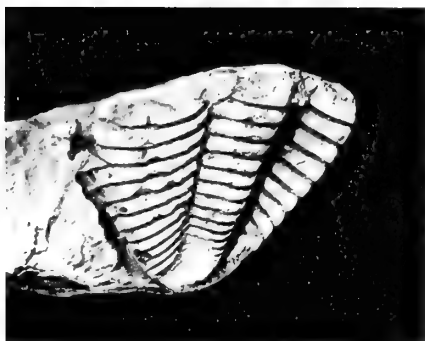
FIG. 8. External mould of right librigena. In. 56787. $\times 4$. Locality λE .

FIG. 9. Internal mould of incomplete cranidium. In. 56799. $\times 3$. Locality λG .

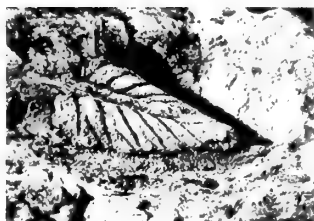
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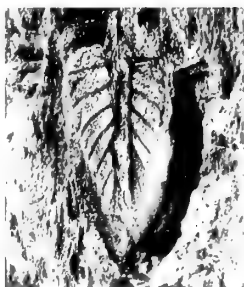
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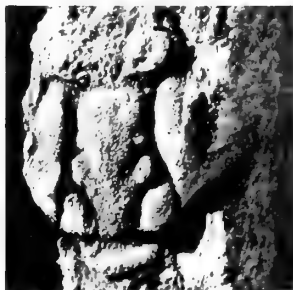
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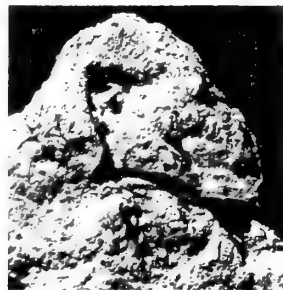
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PLATE 2

- Encrinurus kingi* sp. nov. p. 53
- FIG. 1. Internal mould of holotype pygidium. SM., A. 51706. $\times 2$. Locality λ F.
- FIG. 2. Internal mould of fragmentary paratype pygidium showing tip. In. 56993. $\times 2.5$. Locality λ F.
- FIG. 7. Internal mould of paratype pygidium showing axial and ring furrows. In. 56791. $\times 2.5$. Locality λ F.
- Atractopyge* sp. p. 55
- FIGS. 3, 5. Dorsal and lateral views of internal mould of incomplete cranidium. Sedgwick Museum. A. 51707. $\times 2$. Locality λ G.
- Cyrtolites* cf. *nodosus* (Salter) p. 57
- FIG. 4. Lateral view of internal mould. PG. 3579. $\times 1.5$. Locality λ B1.
- Cryptothyris* cf. *paracyclica* (Bancroft) p. 55
- FIG. 6. Internal mould of slightly distorted brachial valve. BB. 30070. $\times 2$. Locality λ K.
- Strophomena* sp. p. 56
- FIG. 8. Internal mould of pedicle valve. SM., A. 51708. $\times 2$. Locality λ K.
- Rafinesquina* (s.l.) sp. p. 56
- FIG. 9. Internal mould of pedicle valve. BB. 30071. $\times 2$. Locality λ G.
- Sowerbyella* cf. *sericea* (J. de C. Sowerby) p. 56
- FIG. 10. Internal mould of brachial valve. BB. 29807. $\times 1.5$. Locality λ B2.
- FIG. 11. Internal mould of pedicle valve. BB. 29806. $\times 1.5$. Locality λ B2.

All specimens from the Stile End Beds.



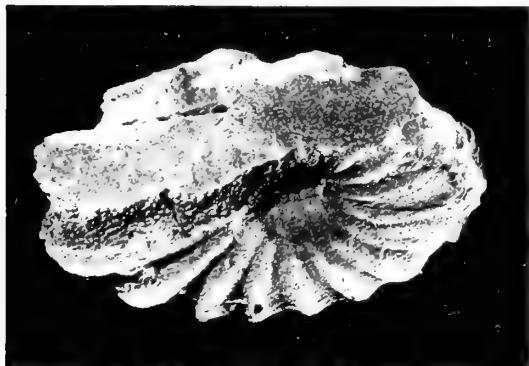
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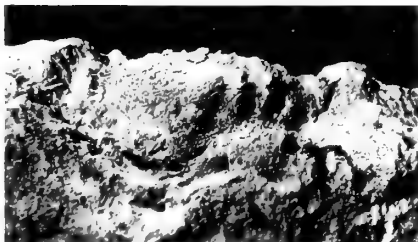
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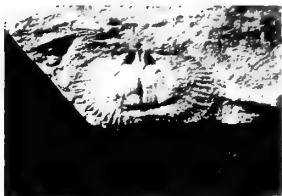
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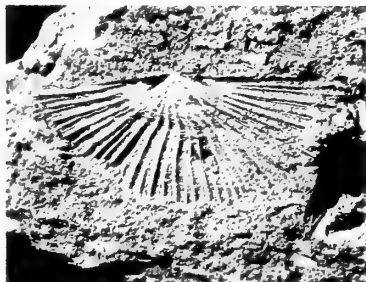
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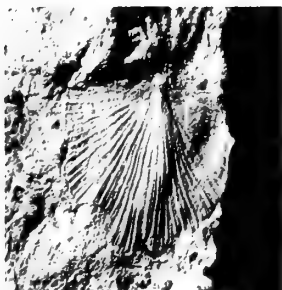
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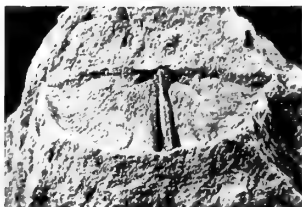
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PLATE 3

Hedstroemina cf. *robusta* (Bancroft) p. 56

FIG. 1. Internal mould of pedicle valve. SM., A. 51709. $\times 1.25$. Locality λG .

FIG. 2. Specimen showing internal mould of pedicle valve and external mould of brachial valve. BB. 29819. $\times 1.25$. Locality λG .

FIG. 3. External mould of brachial valve together with cardinal area. BB. 29816. $\times 1.25$. Locality λG .

Platystrophia sp. p. 56

FIG. 4. Internal mould of longitudinally compressed pedicle valve. SM., A. 51710. $\times 2$. Locality λG .

FIG. 7. Internal mould of pedicle valve. BB. 29809. $\times 1.5$. Locality λG .

Nicolella cf. *actoniae* (J. de C. Sowerby) p. 56

FIG. 5. External mould of brachial valve. BB. 29815. $\times 1.5$. Locality λG .

FIG. 9. Internal mould of fragmentary pedicle valve. BB. 29813. $\times 2$. Locality λC .

Orthis indet. p. 57

FIG. 6. Internal mould of pedicle valve. BB. 29825. $\times 2$. Locality λB_2 .

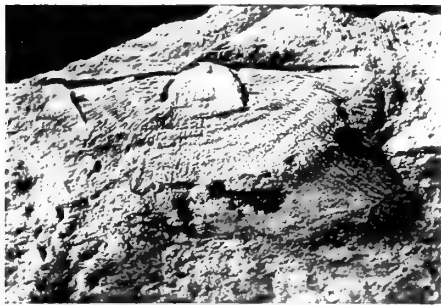
Leptaena sp. p. 56

FIG. 8. Internal mould of pedicle valve. BB. 29812. $\times 1.5$. Locality λB_1 .

Biscuspina sp. p. 56

FIG. 10. Internal mould of brachial valve. BB. 29804. $\times 2$. Locality λG .

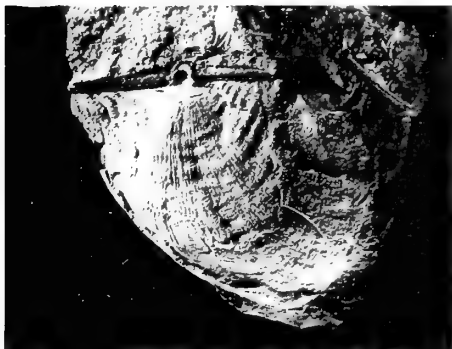
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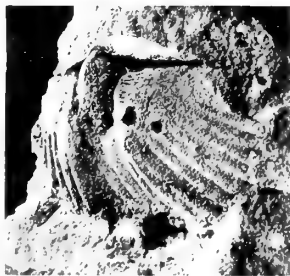
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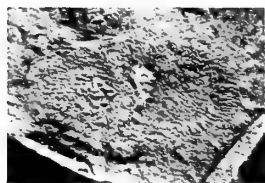


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PLATE 4

- FIG. 1. Latex cast of conjoined dorsal and ventral valves. BB. 30117. $\times 2.7$. Locality 7.
Chonetoides sp. p. 62
 Trilobite gen. et sp. indet. p. 62
- FIG. 2. Internal mould of crushed pygidium listed by Elles & Wood (1895) as *Stygina murchisoniae*. SM., A. 40164. $\times 2$.
- FIG. 7. As for Fig. 2. SM., A. 40163. $\times 2$.
Lonchodomas sp. p. 61
- FIG. 3. External mould of distorted cranidium. SM., A. 40125. $\times 2.5$.
- FIG. 6. Internal mould of incomplete cranidium, listed by Elles & Wood (1895) as *Dindymene ornata*. SM., A. 40142. $\times 7$.
- FIG. 10. Internal mould of cranidium, with external mould of calymenid pygidium. SM., A. 53146. $\times 2$.
- FIG. 11. Internal mould of pygidium, with external mould of dalmanellid brachiopod. SM., A. 40124. $\times 2$.
- FIG. 12. Internal mould of cranidium. SM., A. 40146. $\times 2$.
Primaspis cf. *semievoluta* (Reed) p. 62
- FIG. 4. Internal mould of compressed cranidium. In. 56880. $\times 4$. Locality 1.
Flexicalymene cf. *caractaci* (Salter) p. 62
- FIG. 5. Internal mould of fragmentary, distorted cranidium. SM., A. 40136. $\times 2.25$.
- FIG. 9. Internal mould of incomplete cranidium. SM., A. 40133. $\times 5$.
Brongniartella cf. *bisulcata* (M'Coy) p. 62
- FIG. 8. Latex cast of cranidium. In. 56981. $\times 1.25$. Locality 9.
Lingulella? sp. p. 62
- FIG. 13. External mould, listed by Elles & Wood, 1895 as *Lingula ovata*. SM., A. 40090. $\times 2.5$.
- Kloucekia apiculata* (M'Coy) p. 62
- FIG. 14. Internal mould of distorted cephalon and thorax, listed by Elles & Wood (1895) as *Phacops* sp. SM., A. 40145a. $\times 1.25$.

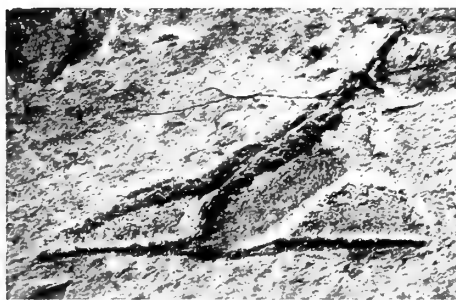
All the specimens derive from the Drygill Shales but, excluding Figs. 4 and 8, all are from old collections and unlocalised with regard to their exact position at Dry Gill.



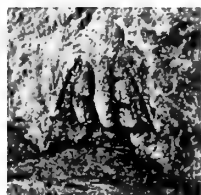
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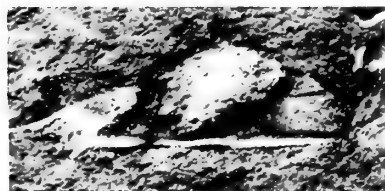
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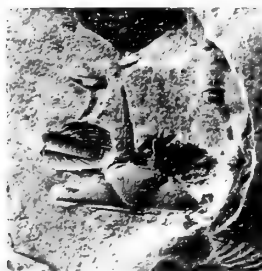
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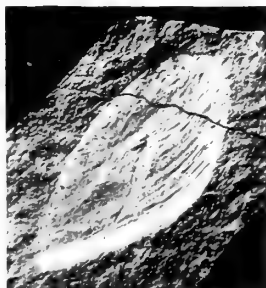
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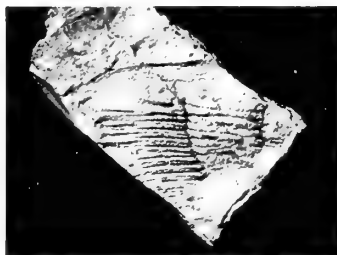
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PLATE 5

Broeggerolithus nicholsoni (Reed) p. 61

- FIG. 1. Internal mould of incomplete cranidium. In. 56982. $\times 2$. Locality 6.
 FIG. 2. Internal mould of pygidium. In. 56983. $\times 3.5$. Locality 1.
 FIG. 5. Internal mould of cranidium. In. 56986. $\times 2.5$. Locality 9.
 FIG. 8. Internal mould of fragmentary cranidium. In. 56989. $\times 2.5$. Locality 6.
 FIG. 9. External mould of underside of cephalic fringe and left librigenal spine. In. 56990.
 $\times 1.5$ Locality 7.
 FIG. 11. External mould of two incomplete dorsal exoskeletons. In. 56992. $\times 1.7$.
 Locality 3.

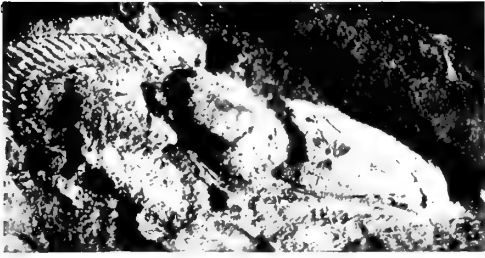
Brongniartella minor (Salter) p. 62

- FIG. 3. Internal mould of pygidium. In. 56984. $\times 2.25$. Locality 6.
 FIG. 6. As for Fig. 3. In. 56987. $\times 2$. Locality 4.
 FIG. 10. Internal mould of incomplete cranidium. In. 56991. $\times 2.5$. Locality 2.

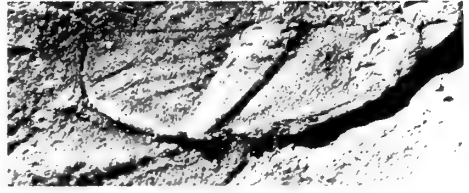
Kloucekia apiculata (M'Coy) p. 62

- FIG. 4. Latex cast of pygidium, showing long terminal spine. In. 56985. $\times 2$. Locality
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 FIG. 7. Internal mould of incomplete, distorted cephalon. In. 56988. $\times 2.5$. Locality 2.

All specimens from the Drygill Shales of Dry Gill.



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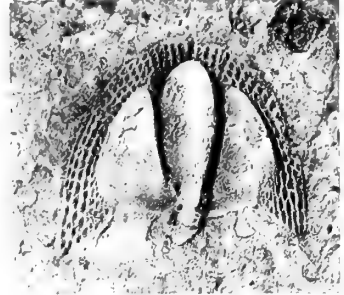
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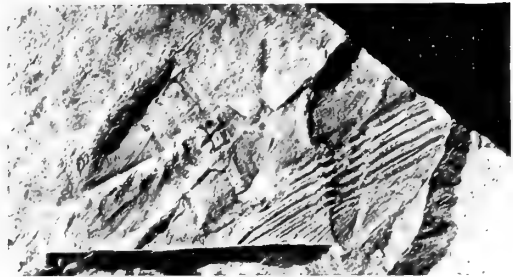
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ON THE SKULL OF
OLIGOKYPHUS

A. W. CROMPTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 9 No. 4

LONDON: 1964

ON THE SKULL OF
OLIGOKYPHUS

BY

ALFRED WALTER CROMPTON, D.Sc.

Director of the South African Museum, Cape Town

Pp. 67-82 ; 1 Plate ; 17 Text-figures

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued February, 1964

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ON THE SKULL OF *OLIGOKYPHUS*

By ALFRED WALTER CROMPTON

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SYNOPSIS

Kühne (1956) gave a reconstruction of the brain-case of *Oligokyphus*. A new reconstruction has been based upon small fragments of the skull; it shows that the two right-angled bends in the ventral surface of the brain-case, described by Kühne, are present only in the particular specimen upon which his reconstruction was based and are due to post-mortem distortion.

There follows a discussion of the spatial relationship of the quadrate to the otic bones and to the squamosal in various cynodonts, both primitive and advanced. This indicates that in *Oligokyphus* the quadrate was *not* suspended from the hinder of the two compartments in the ventral surface of the squamosal, as suggested by Kühne, but from the lateral surface of the anterior process of the paroccipital process.

I INTRODUCTION

KÜHNE (1956) described in great detail fragments of several skulls and post-cranial skeletons of the therapsid *Oligokyphus* Hennig 1922, all from the Liassic fissure "Mendip 14" near Shepton Mallet in Somerset. His excellent monograph includes fairly complete reconstructions of this material. Thus *Oligokyphus* is better known than are many other therapsids of which material is abundant and well preserved.

Oligokyphus is one of the last survivors of the therapsids. Although it has a specialized dentition and many other features which preclude it from being ancestral to any known mammal, it is of the greatest importance for the understanding of the evolutionary trends in the mammal-like reptiles and for the interpretation of the transition from reptiles to mammals.

II. KÜHNE'S RECONSTRUCTION OF THE BRAIN-CASE

As reconstructed by Kühne (1956: 57, text-figs. 17-20), the brain-case of *Oligokyphus* possesses several features which distinguish it from the brain-cases of all other known therapsids—especially the advanced forms *Bienotherium* Young 1940 (see Young 1947) and *Diarthrognathus* Crompton 1958—and of early mammals such as *Triconodon* Owen 1859 (see Kermack 1963). These are as follows:

- (1) The ventral surface of the basioccipital is bent into a right angle, so that the morphologically ventral surfaces of the basisphenoid and of the anterior

part of the basioccipital lie in a vertical plane and face posteriorly. The basipterygoid processes are therefore directed vertically downwards rather than forwards.

- (2) The junction of the vertically orientated ventral surface of the basisphenoid and of the horizontally orientated ventral surface of the parasphenoid also forms a right angle.
- (3) The pituitary fossa opens forwards and slightly downwards.
- (4) The supraoccipital forms a horizontal roof to the posterior part of the cranial cavity.

Kühne's reconstruction, however, introduces a major difficulty which was not discussed in his monograph. If, as he supposed, the basipterygoid processes of *Oligokyphus* were indeed directed ventrally, it would follow that the morphologically ventral surfaces of the posterior ends of the epipterygoids and pterygoids would also lie in a vertical plane. How, then, could they have joined on to the more anterior bones of the palate? (Kühne, unfortunately, did not attempt a reconstruction of the brain-case in lateral view.)

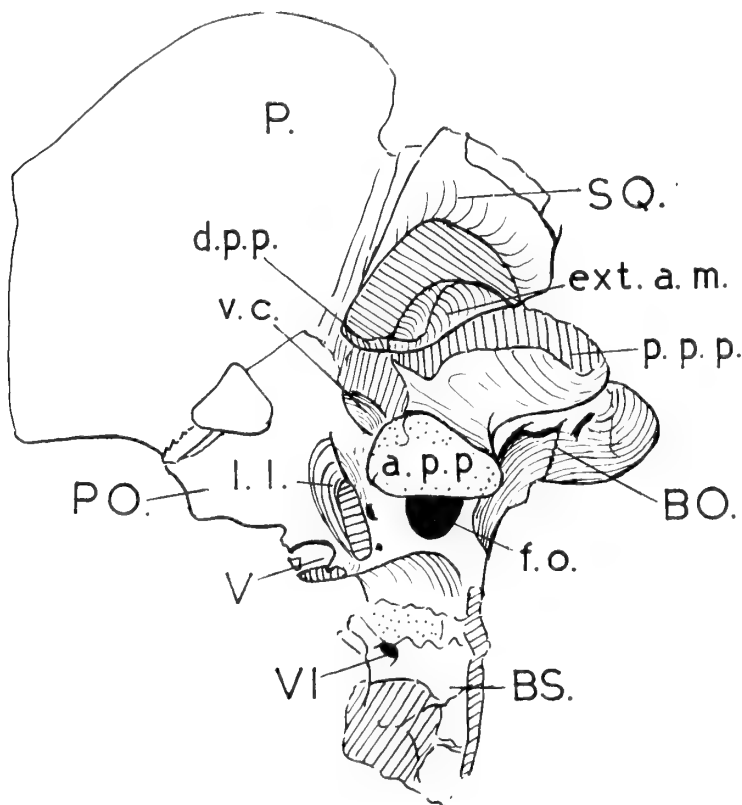
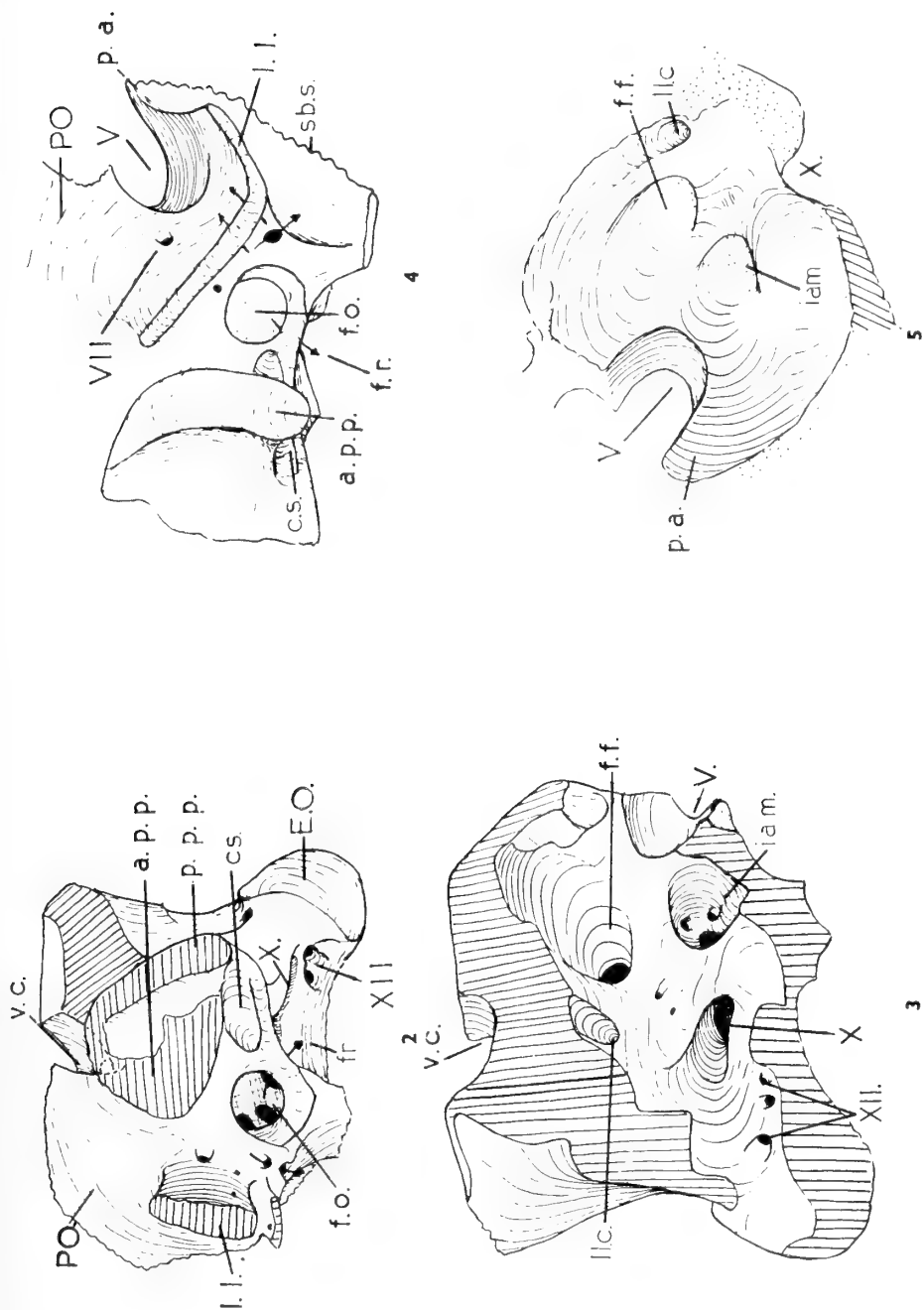


FIG. 1. *Oligokyphus* sp. Partly dislocated brain-case R.7090.
Key to lettering, p. 82.



FIGS. 2-5. *Oligokyphus* sp. Fragments of brain-cases upon which the reconstruction of the brain-case, shown in Text-figs. 6-8, was partly based :

Fig. 2. External view of R.7110. Fig. 3. Internal view of the same. Fig. 4. External view of R.7109.

Fig. 5. Internal view of the same. Key to lettering, p. 82.

At this point it must be noted that Kühne's reconstruction of the hinder part of the skull was based largely upon one incomplete specimen (Brit. Mus. (Nat. Hist.) Palaeont. Dept. No. R.7090 ; Text-fig. 1), of which the bones seemed to be preserved in their natural articulation, not even partly separated. Such articulated skulls are rare among the *Oligokyphus* material.

I cannot agree that the arrangement of the individual bones in R.7090 is as it was in life. The specimen has several large cracks passing through it ; for example, there is a large transverse fracture through the basioccipital (BO.). Moreover, in many cases it is clear that adjacent bones have been separated from one another before fossilization, the best example of this being the wide separation of the squamosal (SQ.) from its contact with the anterior process of the paroccipital process (a.p.p.). Kühne observed that the lower surface of the squamosal bore a marked depression (d.p.p.), into which fitted—so he concluded—the dorsal surface of the anterior portion of the paroccipital process ; but pl. 9, fig. 4 of his monograph shows a distinct gap between those two elements, apparently filled with plaster. The presence of this gap suggests that in R.7090 the parietal (P.) and squamosal have been moved dorsally relative to the remainder of the specimen ; such movement could account for the vertical orientation of the morphologically ventral surface of the basisphenoid (BS.). The horizontal orientation of the supraoccipital appears also to be the result of dislocation. But, since the exact nature of the relative movement between its dorsal and ventral components cannot be ascertained, R.7090 should not be used as a basis upon which to reconstruct the brain-case of *Oligokyphus*.

III. NEW RECONSTRUCTION OF THE BRAIN-CASE (FROM FRAGMENTS)

The collection of *Oligokyphus* material in the British Museum (Natural History) includes several small fragments of the brain-case and adjacent elements, beautifully preserved and apparently not much distorted. Kühne listed these (p. 46) and figured some of them. Two of them are shown in Text-figs. 2-5.

Using these fragments, I have prepared a new reconstruction of the brain-case (together with certain associated bones such as the quadrate and squamosal) ; this reconstruction is shown in Text-figs. 6-8. The task was difficult because the fragments represent several individuals of unequal size. Pieces from different parts of the region were therefore photographed from the same angle ; drawings were prepared from the photographs, the enlargement of the drawings being adjusted to compensate for the varying sizes of the individuals concerned. The three views of the reconstructed brain-case were made by superimposing these drawings.

The lateral view (Text-fig. 6) is based mainly upon the fragments numbered R.7109 and R.7110 (Text-figs. 4 and 2 respectively). The ventral surface of the basioccipital is reconstructed from R.7113, the parietal from R.7090 and the squamosal from R.7088 and R.7090. The combined reconstruction based upon

these fragments does *not* show two right-angled bends in the base of the skull ; a sagittal section of the ventral surface of the basioccipital and the basisphenoid would form an S-shaped curve, the ventral surface of the basisphenoid being lower than that of the basioccipital. Both R.7110 and R.7113 show a duct (v.c.) through the lateral wall of the brain-case just above the paroccipital process (Text-figs. 2, 6), its external opening lying close to the anterior opening of the post-temporal fenestra (pt.f.). According to Brink (1955), a similar foramen is present in cynodonts (Text-figs. 10, 12) ; while Ginsburg (1962 : 188-189) described a similar duct in the tritylodontid *Likhoelia ellenbergeri*, and named it the floccular canal.

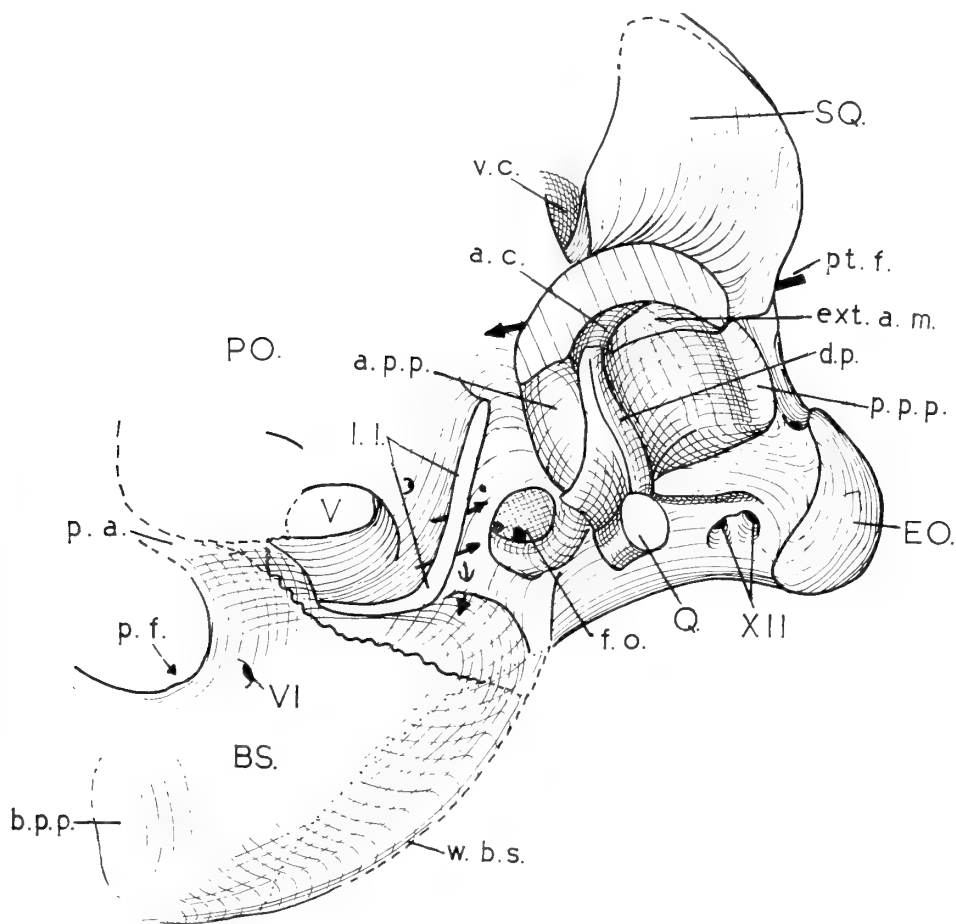


FIG. 6. *Oligokyphus* sp. Reconstruction of the brain-case, in lateral view. Key to lettering, p. 82.

The internal view of the reconstructed brain-case (Text-fig. 7) is based mainly upon R.7090, R.7109 (Text-fig. 5), R.7110 (Text-fig. 3), R.7113 and R.7242. It affords no evidence to support either of Kühne's beliefs, that there were two right-angled bends in the base of the skull and that the supra-occipital (SO.) formed a horizontal roof to the posterior part of the cranial cavity. The duct through the cranial wall above the paroccipital process opens internally just above and behind the floccular fossa (f.f.) ; in R.7090, where the external opening of this duct is

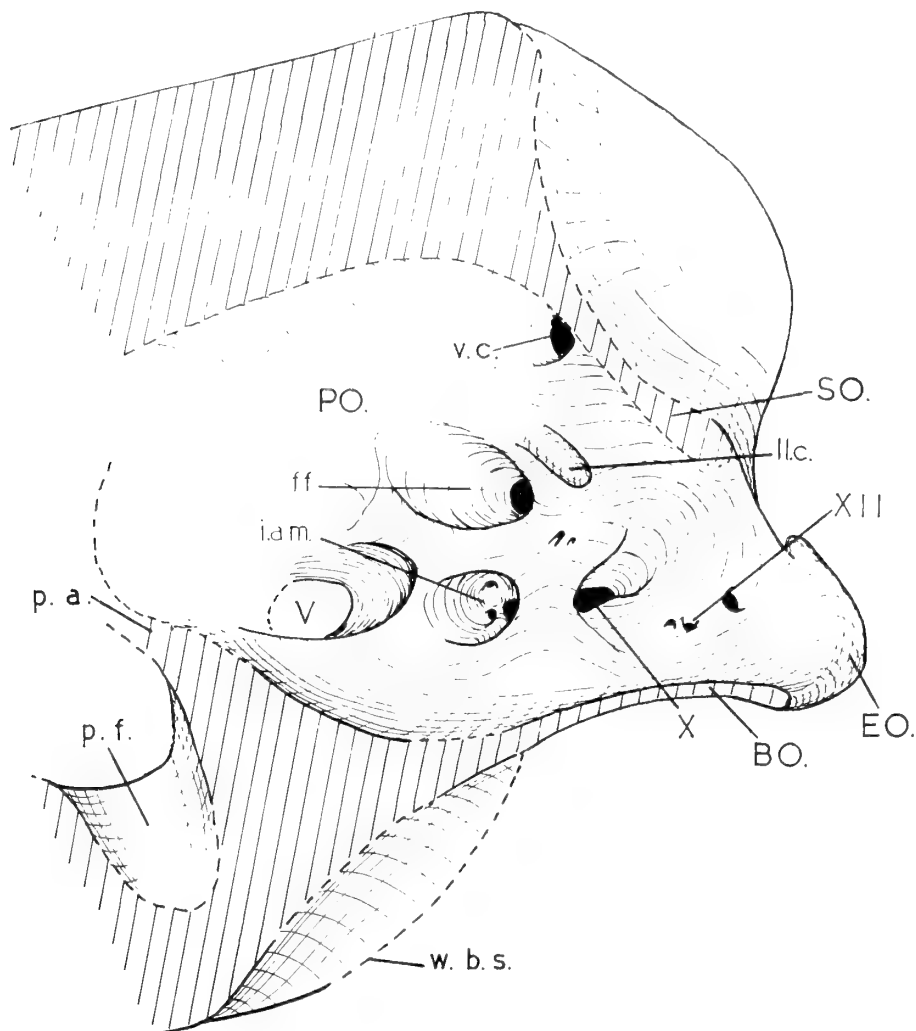


FIG. 7. *Oligokyphus* sp. Reconstruction of the brain-case : section in the sagittal plane, to show the interior.
Key to lettering, p. 82.

clearly visible (Text-fig. 1), its internal opening has been obscured by the downward displacement of the supraoccipital.

The ventral view (Text-fig. 8) is based mainly upon R.7088, R.7109, R.7113 and R.7242. The most marked feature of the *Oligokyphus* basisphenoid is that its ventro-lateral edges are drawn downwards and outwards as two thin sheets or wings of bone (w.b.s.), which form a partial floor to the cavum epiptericum on either side of the skull. This condition contrasts with that found in cynodonts, where the ventrolateral edges of the basisphenoid project for only a short distance.

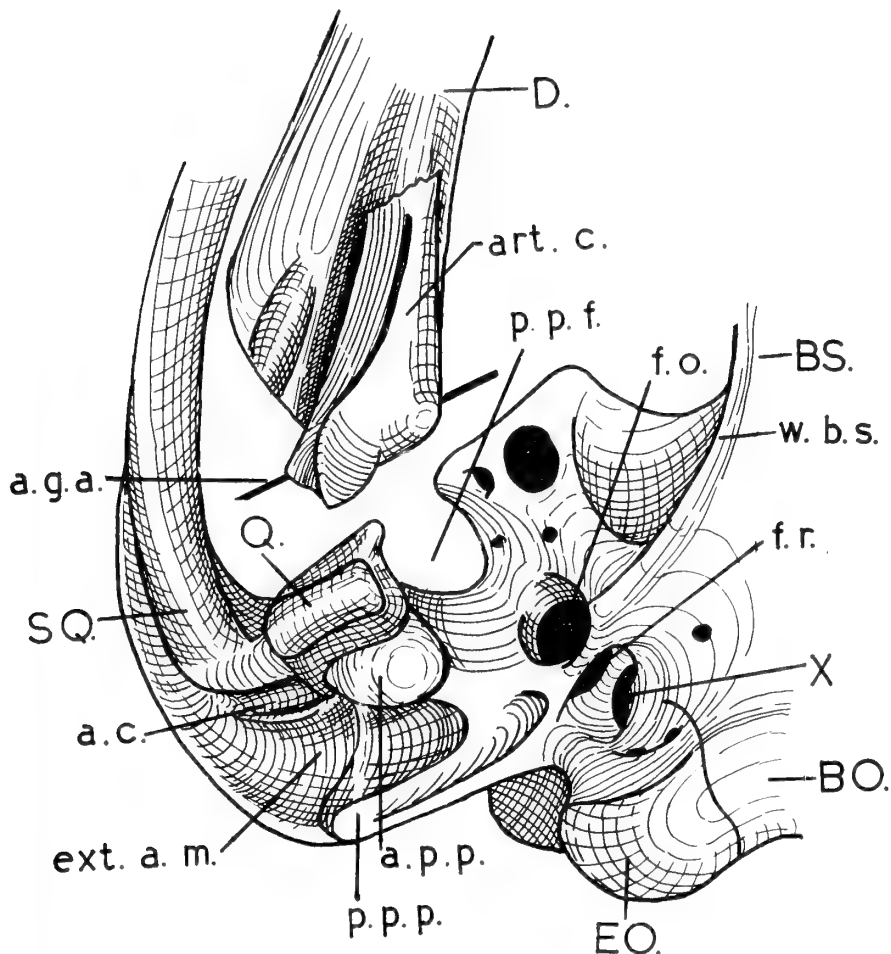


FIG. 8. *Oligokyphus* sp. Reconstruction of the brain-case and hind part of the lower jaw, in ventral view.

Key to lettering, p. 82.

In general, however, the brain-case of *Oligokyphus* (as reconstructed in Text-figs. 6-8) does not differ greatly from the brain-cases of primitive cynodonts, advanced cynodonts, *Bienotherium* or *Diarthrognathus*. Comparison is facilitated by Text-figs. 9-17, which show the brain-cases of a procynosuchid, *Cynognathus* and *Oligokyphus* in ventral, lateral and occipital views.

Ginsburg (1962) published an account of a new tritylodontid, *Likhoelia ellenbergeri* Ginsburg 1961, from the upper part of the Red Beds (Upper Trias) of Basutoland. The material included an almost complete brain-case, in which the ventral surface of the basioccipital was not bent into a right angle. Ginsburg remarked upon the ventral keel of the basisphenoid of *Oligokyphus* and concluded that it was sufficient to rotate the whole posterior part of the skull of *Oligokyphus* through some 30° to obtain a cranium very like those of *Bienotherium* and of *Likhoelia*.

IV. THE ANTERIOR WALL OF THE PROOTIC

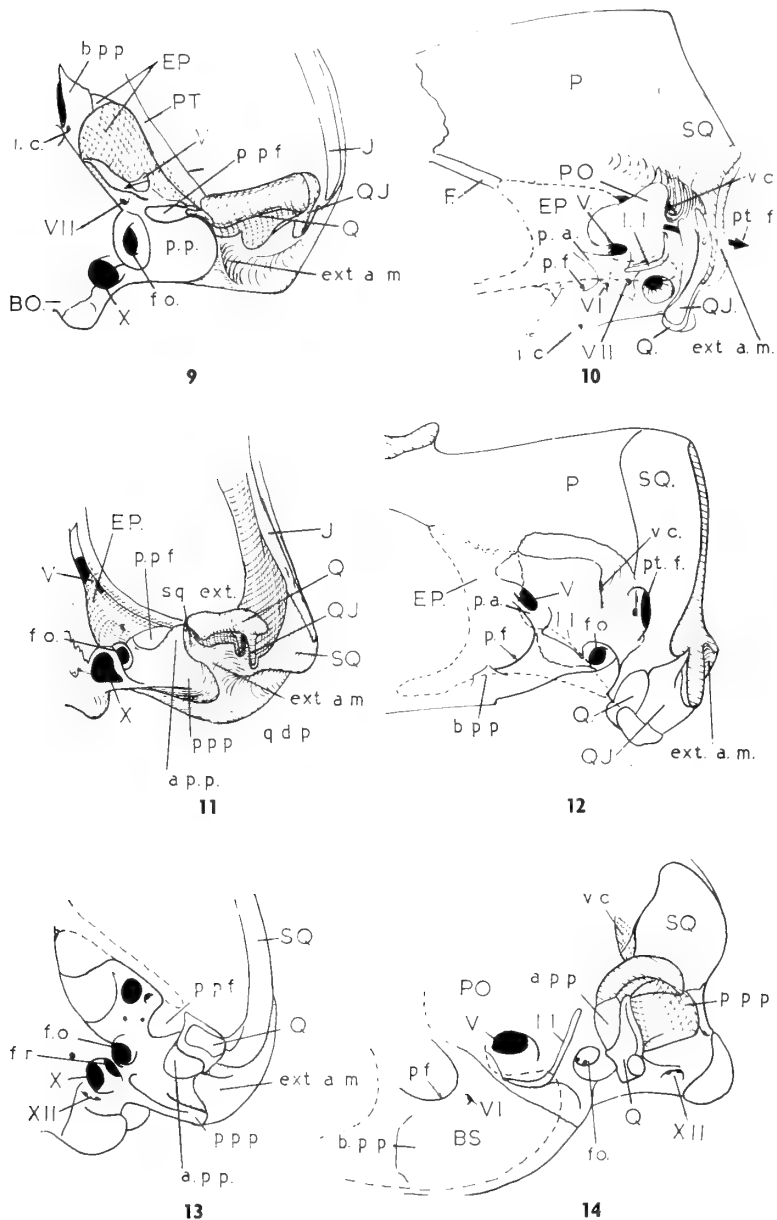
In Text-figs. 6 and 7 the anterior wall of the prootic (PO.) of *Oligokyphus* has been reconstructed in such a way that it completely encloses a foramen (V.) for the trigeminal nerve. There is no conclusive evidence for this reconstruction, for in none of the skull fragments is the anterior border of the prootic preserved entire.

The anterior border of the prootic is best preserved in R.7109 (Text-fig. 4), where the antero-ventral corner of the bone, above the opening for the trigeminal nerve, is directed downwards and forwards towards the ossified pila antotica (p.a.). The dorsal surface of the pila antotica is smooth except for its postero-dorsal tip, which has a broken surface; this may indicate that the antero-ventral corner of the prootic, above the trigeminal nerve, extended downwards and forwards in life towards the pila antotica and thus enclosed the nerve. In the early mammal *Morganucodon* the anterior border of the prootic formed a foramen for the trigeminal nerve (Kermack & Mussett 1958). In *Likhoelia* the anterior lamina of the prootic appears to enclose a foramen pseudovale, although it may be that the anterior border of the foramen in question is formed by the epipterygoid; the sutures cannot be distinguished in this region.

V. THE POSITION OF THE QUADRATE

The condyle of the quadrate (Q.) (Text-figs. 6, 8, 17) supports a vertical sheet of bone which runs more or less transversely. The upper margin of this sheet expands in the horizontal plane to form a smooth concave surface, facing upwards; at its lateral end, however, it rises into the high "peg-like process" (d.p.) mentioned by Kühne (pp. 39, 40). The smooth concave surface, lying immediately above the quadrate condyle, is confluent with the medial surface of the peg-like process.

Kühne claimed (p. 45) that there was no place on the periotic that could have served for the attachment of the quadrate. But the ventral surface of the posterior part of the squamosal bears an ectotympanic cavity which is divided into two compartments (Text-fig. 8, ext.a.m., a.c.). He therefore concluded that "... there is no other possible place for the quadrate and the quadrato-jugal than the anterior end of the two compartments ..."; that is, the anterior compartment would be for the quadrato-jugal and the posterior compartment for the quadrate.



FIGS. 9-14. Comparisons of the brain-cases of cynodonts and of *Oligokyphus* in ventral and lateral views :

Figs. 9, 10. *Leavachia* (a procynosuchid). Figs. 11, 12. *Cynognathus*.

Figs. 13, 14. *Oligokyphus*.

Key to lettering, p. 82.

Kühne also pointed out (p. 40) that the dorsal surface of the quadrate and the dorsal surface of the peg-like process had no corresponding articular surfaces on the squamosal. Because, in particular, the posterior compartment of the ectotympanic cavity did not possess an articular surface for the dorsal surface of the quadrate, he decided that the connection between the quadrate and the squamosal must have been maintained by ligaments.

But the ectotympanic cavity on the ventral surface of the squamosal is continuous with the external auditory meatus. If the quadrate really had been attached to the squamosal by ligaments, with its peg-like process fitting into the posterior compartment of the ectotympanic cavity, then it would partly have blocked the external auditory meatus. Further, with the quadrate in the position suggested by Kühne, the glenoid facet of the articular complex would not have reached the quadrate condyle; it would have been prevented from doing so by the anterior process of the paroccipital process, which lies antero-medial to the posterior compartment (Text-fig. 8).

A study of the relative positions of the articular and the quadrate in cynodonts throws some light on the probable position of the quadrate in *Oligokyphus*.

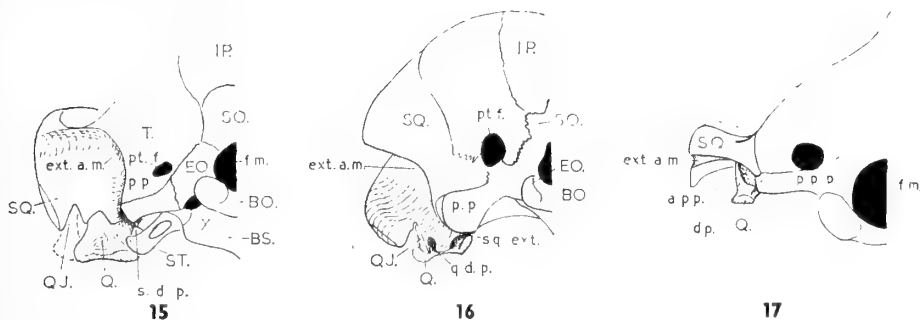
In the procynosuchids of the Upper Permian (Text-figs. 9, 10, 15) the quadrate is suspended partly from the squamosal and partly from the paroccipital process; the latter (Text-fig. 9, p.p.) is fairly slender antero-posteriorly. The quadrate and quadrato-jugal fit into a shallow pocket in the anterior surface of the squamosal, and the ventral edge of the squamosal is notched. The medial surface of the quadrate abuts against the antero-lateral surface of the paroccipital process; this feature, which has been observed in several procynosuchids and other early therapsids, is seen well from behind (Text-fig. 15). The antero-medial surface of the quadrate meets the quadrate rami of the pterygoid (PT.) and epipterygoid (EP.). The external auditory meatus (ext.a.m.) of early cynodonts is not deep, but its course is clearly shown in Text-figs. 9 and 15; it follows the dorsal surface of the squamosal, passes above the medial quadrate condyle, runs vertically downwards, and ends just by the lower surface of the postero-lateral corner of the paroccipital process. Cox (1959) named this corner the tympanic process in anomodonts. The stapes of a procynosuchid is exemplified by the specimen of *Leavachia microps* (Broom & Robinson 1948) illustrated in Text-fig. 15, in which the bone (ST.) is preserved in position. It bears a distinct blunt process, directed laterally, which probably supported a cartilaginous extra-stapedial process (Parrington 1946); it has also a well preserved dorsal process (s.d.p.).

In later cynodonts, e.g. *Cynognathus* of the Lower Trias (Text-figs. 11, 12, 16; Pl. 1), several significant developments have taken place. It can be seen from behind (Text-fig. 16) that the depth of the squamosal has increased greatly and that the external auditory meatus has also become deeper. Ventral and occipital views show that a thin flange of the squamosal (sq.ext.) extends downwards and forwards, completely covering the lateral surface of the paroccipital process; the latter is therefore no longer in contact with the greatly reduced quadrate. The external auditory meatus has been extended downwards and forwards by the extension of

the squamosal in that same direction, and it ends just above the medial condyle of the quadrate ; its most ventral part lies lateral to the centre of the ventral part of the lateral surface of the paroccipital process (Text-fig. 11). The posterior surface of the quadrate, above the medial condyle, is slightly concave. A short flange orientated in an antero-posterior plane (Text-fig. 16, q.d.p.) extends upwards from the lateral side of the quadrate, its postero-dorsal corner fitting into a pocket in the ventral surface of the squamosal. The quadrato-jugal (QJ.) consists mainly of a high, flat sheet, also orientated antero-posteriorly, lying against the quadrate (Text-fig. 12) ; ventrally it is fused with the quadrate above the lateral condyle. On its medial side the posterior edge of the vertically orientated quadrato-jugal lies against a ventrally directed process of the squamosal (Text-figs. 11, 16) ; a shallow notch in the ventral surface of the squamosal contains only the postero-dorsal tip of the quadrato-jugal. A stereo-photograph of this region of the skull of *Cynognathus* (Pl. 1) may help to explain the relationship of the quadrate to the squamosal.

In *Cynognathus* (Text-fig. 11) the lateral region of the paroccipital process is wider antero-posteriorly than in procynosuchids. The ventral surface of the paroccipital process of *Cynognathus* can be divided into two regions, a bulbous anterior region (a.p.p.) and a flat posterior region (p.p.p.) ; the quadrate lies lateral to the former. In *Oligokyphus* (Text-fig. 13) the paroccipital process ends laterally in two distinct processes, a bulbous anterior process and a narrow posterior process, separated by a shallow depression. It is reasonable to conclude that the bulbous anterior process of the paroccipital process of *Oligokyphus* is homologous with the bulbous anterior region of the paroccipital process of *Cynognathus*.

One of the major differences between *Oligokyphus* and cynodonts such as *Cynognathus* is in the height of the squamosal, which is much reduced in *Oligokyphus* ; this is best shown by a comparison of the respective occipital views (Text-figs. 16, 17). There is a similar reduction in *Diarthrognathus*. The squamosal of *Oligokyphus*, because of this reduction in height, does not cover the lateral surface of the paroccipital process (Text-fig. 6).



FIGS. 15-17. Comparison of the brain-cases of cynodonts and of *Oligokyphus* in occipital view :

Fig. 15. *Leavachia*. Fig. 16. *Cynognathus*. Fig. 17. *Oligokyphus*.

Key to lettering, p. 82.

As the quadrate of advanced cynodonts is suspended from the squamosal, a reduction of the ventral part of the latter would cause the quadrate to lose its only firm attachment. If, however, the quadrate migrated very slightly towards the mid-line, it could establish alternative contact with the lateral surface for the anterior part of the paroccipital process.

In *Oligokyphus* the quadrate has a smooth concave dorsal surface and a dorsally directed peg-like process on its lateral surface. This peg-like process is perhaps homologous with the dorsally directed process above the lateral condyle of the cynodont quadrate. The concave dorsal surface of the *Oligokyphus* quadrate could have evolved by the further development of the concavity which, in *Cynognathus*, is already present in the posterior surface of the quadrate above the condyle.

The smooth concavity of the *Oligokyphus* quadrate, formed by its dorsal surface and by the medial surface of the peg-like process, fits perfectly against the lateral and ventro-lateral surface of the bulbous anterior head of the paroccipital process (Text-figs. 6, 8, 17). Further, this would be the expected position of the quadrate if, in the ancestors of *Oligokyphus*, the squamosal had been reduced in height and no longer suspended the quadrate. The shape of the quadrate in *Oligokyphus* confirms that it was supported by the anterior process of the paroccipital process. If the quadrate be placed in this position the transverse axis of its condyle is oblique to the sagittal plane (Text-fig. 8), not perpendicular thereto as is usual in cynodonts (Text-figs. 11, 13); this accords with the oblique orientation of the articulating surface of the articular. In Text-fig. 8 the articular complex and the back end of the dentary are shown from below; the transverse axis through the glenoid (a.g.a.) is parallel to that through the quadrate condyle.

In *Cynognathus* the external auditory meatus lies entirely within the squamosal, with its lower part lateral to the centre of the lateral surface of the paroccipital process. In *Oligokyphus*, however, the squamosal is reduced and can no longer delimit the external auditory meatus lateral to the paroccipital process; but there is a hollowing in the lateral surface of the paroccipital process, continuous with the external auditory meatus in the squamosal, which presumably helped to delimit the lower part of the meatus. It is this hollowing which divides the paroccipital process into anterior and posterior processes. The external auditory meatus of *Oligokyphus* would therefore have ended behind the medial condyle of the quadrate, just as in cynodonts. These arguments seem to support the view that the quadrate was not suspended from the posterior compartment on the ventral surface of the squamosal. It is possible, however, that the dorsal end of the peg-like process on the quadrate may have extended into the anterior compartment.

The advanced therapsid (early mammal?) *Diarthrognathus* seems also to have a lower squamosal. The withdrawal of the quadrate into the middle ear in early mammals may be correlated with a reduction of the paroccipital process.

VI. ACKNOWLEDGMENTS

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KEY TO LETTERING

a.c.	anterior compartment	p.a.	pila antotica
a.g.a.	axis of the articular glenoid	p.f.	pituitary fossa
a.p.p.	anterior process of the paroccipital process	PO.	prootic
art.c.	articular complex	p.p.	paroccipital process
BO.	basioccipital	p.p.f.	pterygo-paroccipital foramen
b.p.p.	basipterygoid process	p.p.p.	posterior process of the paroccipital process
BS.	basisphenoid	PT.	pterygoid
c.s.	cavity for stapedial muscle	pt.f.	post-temporal fenestra
D.	dentary	Q.	quadrate
d.p.	dorsal process of the quadrate	q.d.p.	dorsal process of the quadrate
d.p.p.	depression in the squamosal for the paroccipital process	QJ.	quadrato-jugal
EO.	exoccipital	s.b.s.	suture with the basisphenoid
EP.	epipterygoid	s.d.p.	dorsal process of the stapes
ext.a.m.	external auditory meatus	SO.	supraoccipital
F.	frontal	SQ.	squamosal
f.f.	floccular fossa	sq.ext.	ventral extension of the squamosal
f.m.	foramen magnum	ST.	stapes
f.o.	fenestra ovalis	T.	tabular
f.r.	fenestra rotunda	v.c.	venous canal
i.a.m.	internal auditory meatus	w.b.s.	wing of the basisphenoid
i.c.	internal carotid foramen	V	foramen for the trigeminal nerve (incisura prootica)
IP.	interparietal	VI	foramen for the sixth cranial nerve
J.	jugal	VII	foramen for the seventh cranial nerve
l.l.	lateral lamina	X	jugular foramen
l.l.c.	depression for the lateral lobe of the cerebellum	XII	foramina for the twelfth cranial nerve
P.	parietal		



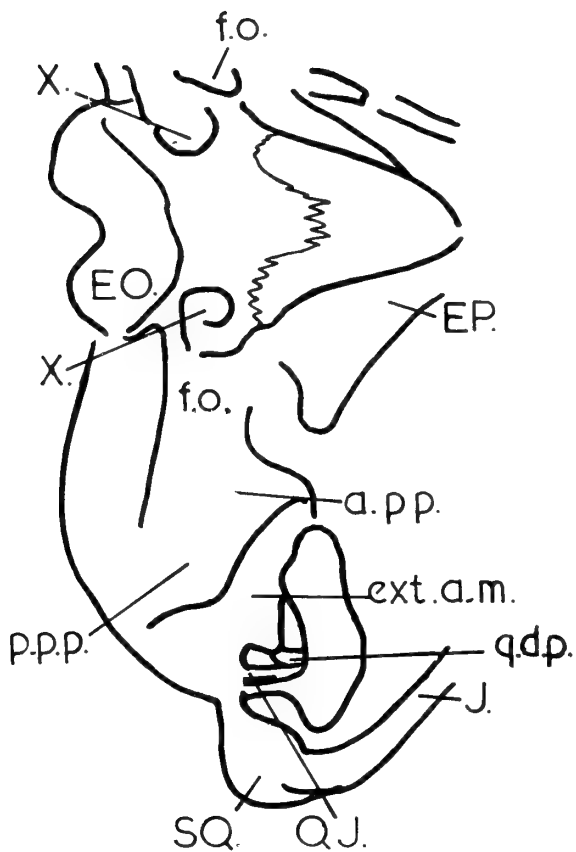
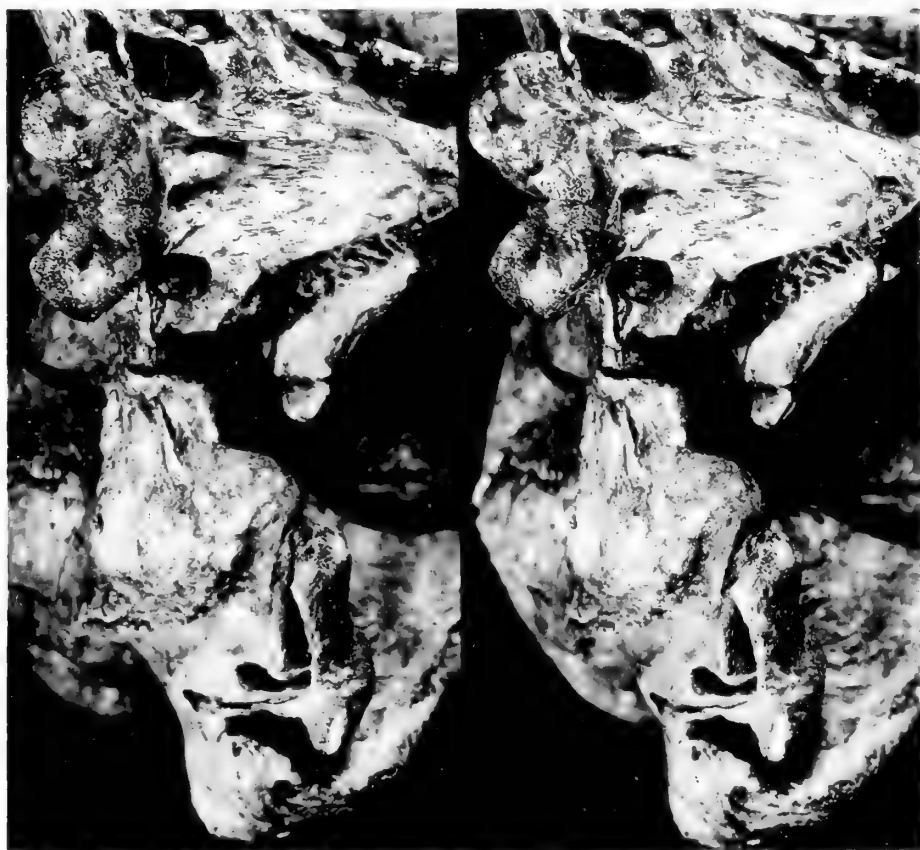


PLATE 1

Cynognathus sp.

Stereo-photographs of the hind part of the skull, in ventral view. $\times 1.25$ approx.

Key to lettering, p. 82.





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THE
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An Historical Survey

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SYNOPSIS

Establishment of man's high antiquity depended on finding undoubted artifacts in deposits of known geological age, and human bones fossilized with extinct animals : discoveries by Boucher de Perthes in Somme gravels and by Schmerling in Belgian caves. Stratified rocks first divided into three age-groups. Lyell subdivided the Tertiary era into five periods on faunal evidence. Living species and signs of man predominated in Post-Pliocene deposits constituting Quaternary era with its ice age. Palaeolithic cultural stage, earlier Quaternary (Pleistocene) ; question of whether any artifacts occur in Tertiary deposits.

Organic content of human bones from Neanderthal and Aurignac cited as dating evidence. Neanderthal skull compared with that from Gibraltar : evidence of an extinct species of man. Moulin-Quignon jaw not fossil. Remains of apes described in early nineteenth century from European Miocene : but idea persisted that man in present form already existed, hence modern skeletons unearthed from Pliocene deposits then uncritically accepted as fossils. Cro-Magnon cave yielded fossil *Homo sapiens*, Late Pleistocene fauna and Upper Palaeolithic industry.

French caves and open sites provided sequences of Palaeolithic industries and faunal stages which served as frameworks for relative dating of fossil man in Europe. Interest shifted to tropics : remains of early Pleistocene *Pithecanthropus* found in Java ; jaw of contemporaneous hominid in Mauer Sands, fauna eventually ranked as basal Middle Pleistocene.

Finally four orders of relative dating (R1, R2, R3, R4) and four orders of " absolute " (chronometric) dating (A1, A2, A3, A4) are defined and applied to the classic fossil hominids

I. ANTIQUITY OF MAN: HISTORICAL BACKGROUND

THE appearance of Darwin's *Origin of Species* in 1859 dramatically focused attention on the whole problem of the origin of living things including man himself. In his autobiography Darwin has recorded that already in the year 1837 or 1838, when he first became convinced that species were mutable productions, he could not avoid the belief that man must come under the same general law. He continued as follows:

"Although in the *Origin of Species*, the derivation of any particular species is never discussed, yet I thought it best, in order that no honourable man should accuse me of concealing my views, to add that by the work in question 'light would be thrown on the origin of man and his history'. It would have been useless and injurious to the success of the book to have paraded without giving any evidence my conviction with respect to his origin."

The first step towards working out the application of his theory to man was to collect the facts, and this he did in preparing his book on *The Descent of Man* (1871). Darwin there stated that it was the establishment of the high antiquity of man that was the indispensable basis for the understanding of his origin; and for the demonstration of this he was indebted to the geologist Sir Charles Lyell, who assembled the facts then available in *The Geological Evidence of the Antiquity of Man* (1863), and to the prehistorian Sir John Lubbock (afterwards Lord Avebury) whose book on *Prehistoric Times* appeared in 1865.

Establishing the antiquity of man depended on two sorts of evidence: recognizable works of man, such as deliberately shaped stones (artifacts), found in geologically datable deposits; and fossilized human remains associated with extinct animals.



FIGS. 1-3. Selection of "ceraunia" figured by Mercati (d. 1593). "Most men" he said "believe that ceraunia are produced by lightning": but he considered they "have been broken from very hard flints . . . in the days before iron was used for the follies of war". Fig. 1, polished stone axe-head (Neolithic). Fig. 2, blade tool (Upper Palaeolithic?). Fig. 3, tanged arrowhead (Bronze Age). All $\times \frac{1}{2}$ nat. size.

The conception that man had a long unrecorded past entered very few minds before the middle of the last century, although the seeds of the idea had been sown by a few men far ahead of their time in earlier centuries, for example Michèle Mercati

who, in the second half of the 16th century,¹ concluded that the stones popularly called *ceraunia* (thunderbolts) were really stone implements made before men had iron (Text-figs. 1-3), the Frenchman Isaac de la Peyrère, whose book *Primi Homines ante Admum* (claiming that *ceraunia* were the work of a pre-Adamite race of man) was publicly burnt in Paris in 1655 ; and the English archaeologist John Frere whose discovery of flint implements in brickearths at Hoxne in Suffolk (Text-fig. 4) led him to infer in 1797² that they had been " used by a people who had not the use of



FIG. 4. Flint hand-axe (Lower Palaeolithic) from deposit containing bones of extinct animals at Hoxne, Suffolk. After J. Frere, 1797. Nat. size. Ashmolean Museum, Oxford.

metals", and belonged "to a very ancient period indeed, even before that of the present world".

The first record of the other class of evidence, association of human bones with extinct animals, was apparently made by Johann Friedrich Esper, who in 1771 discovered in the Gailenreuth caves near Bamberg some human bones associated with cave-bear. In his report on the discovery, published in 1774, he asked this question about the human bones: "Did they belong to a Druid or to an Antediluvian or to a Mortal Man of more recent times?"—and concludes: "I dare not presume without any sufficient reason these human members to be of the same age as the other animal petrifications. They must have got there by chance together with them."³

Esper's scientific caution was admirable, for he hinted clearly enough that he had begun to doubt the current orthodoxy. Not so Professor Johann Scheuchzer of Zürich, who some forty years earlier (in 1731) had described some fossil bones embedded in a layer of shale from Oeningen in Baden as "the bony skeleton of one of those infamous men whose sins brought upon the world the dire misfortune of the deluge". He labelled an illustration of this specimen "*Homo diluvii testis*".⁴ A century later the great French naturalist Cuvier identified the remains as those of an extinct salamander, which was named *Andrias scheuchzeri*—it is of Miocene age, that is to say about 20 million years old.

Cuvier was opposed to the idea of the great antiquity of man. He was one of the leading Catastrophists, believing that the fossil records could only be explained by a series of creations⁵ alternating with catastrophic floods of which the Noachian was the most recent, and he denied that there was any acceptable evidence for the existence of fossilized remains of man. Commenting on some human bones alleged to have been found with remains of diluvial animals in the Rhine Valley, he wrote in 1823: "All the evidence leads us to believe that the human species did not exist at all in the countries where the fossil bones were found, at the period of the upheavals which buried them".

In his work on *Reliquiae Diluvianae* (1823), the Rev. William Buckland, Professor of Geology in the University of Oxford, and a follower of Cuvier, explained the use of the term diluvium for those superficial deposits, gravels, loams and the like produced by the "last great convulsion that has affected our planet". He said that wherever human remains had been discovered in Europe with bones of antediluvian animals, attendant circumstances indicated them to be of *postdiluvian* origin; although he admitted that theoretically human remains might be expected in the diluvium of central Asia—the "cradle of the human race". He judged that the Deluge was of short duration and took place not more than 6,000 years ago. As one of the authors of the Bridgewater Treatises written to illustrate Paley's *Natural Theology* Buckland was hampered by the conception there endorsed that the world had been created about 4004 B.C. He expostulated with John Hunter over his conclusion (published in 1794) that the animal bones in the Gailenreuth caves accumulated through these being occupied by wild beasts during "many thousands of years" (an opinion grounded on the different degrees of preservation of the

bones). According to Buckland this was a grossly excessive estimate—he thought that Hunter should have said many *hundreds* of years.

The tradition of the universal Deluge undoubtedly hindered the progress of geological knowledge for a number of years, but the more enlightened diluvialists eventually saw the impossibility of explaining all the facts in terms of a single flood. Buckland admitted that there must have been many catastrophes besides the Noachian Deluge. The difficulties in which he found himself, inspired the couplet written by one of his ecclesiastical friends :

Some doubts were once expressed about the Flood ;

Buckland arose, and all was clear as . . . mud.

In later life Dean Buckland modified his diluvial theory ; and after accepting Agassiz's demonstration of the action of ice he admitted that some of the deposits in Britain which had been attributed to the deluges were probably the outcome of glacial action.

Just as a revolution in biological thought was brought about by the publication of Darwin's theory of the origin of species by natural selection, so geological thought was revolutionized by Lyell's *Principles of Geology* (1830–1833) which marshalled an immense array of observations indicating that the present is the key to the past. This idea of “ uniformitarianism ” in the physical world was obviously much in line with the principles of continuity and gradual development in the biological sphere expressed by Darwin's theory : just as on the other hand “ catastrophism ” marched with the idea of a series of special creations. Uniformitarianism did not imply that conditions or processes in past ages were always identical with those in the present, but that they were of the same general character, differing only in distribution and degree. Thus, observations on the action of glaciers in the Alps when applied to the interpretation of certain types of deposit (*Drift*) in Britain led to the inference that this country had been affected by an Ice Age. Buckland, in contrast, had remarked in 1823 (p. 227) on “ the total impossibility of referring any of these appearances to the effect of ancient or modern rivers, or any other cause, that are now or appear ever to have been in action, since the retreat of the diluvian waters ”.

At numerous sites in Europe during the first half of the nineteenth century, human bones and artifacts were found with remains of extinct animals, and were being claimed by an unorthodox minority of investigators as indicating man's great antiquity. These finds were not, however, widely accepted as genuine associations so long as the climate of scientific opinion was dominated by creationist or diluvialist doctrines. Some of the claims, particularly those relating to human skeletons, may have been erroneous, but others were genuine enough and were recognized as such by a few unprejudiced minds. In 1823 Buckland himself discovered a human skeleton (which we now know to have been that of a man of the Ice Age) under a covering of red ochre in Goat's Hole, Paviland, in South Wales (Text-fig. 5), but he assumed that it was the skeleton of a British woman dating from about the time of the Roman Conquest. He interpreted the numerous artifacts of mammoth ivory which were in contact with the ribs of this “ Red Lady of



FIG. 5. Goat's Hole, Paviland. *After Buckland, 1823* The human skeleton is shown as lying in a cavity excavated into the deposits containing remains of mammoth (E, F).

Paviland" as indicating that her kinsmen dug up the antediluvian elephant tusks from the floor of the cave and utilised this fossil ivory for making ornaments. Apparently it did not occur to Buckland that the human skeleton and the ivory might have been contemporaneous.

Early discoveries of this kind indicating man's great antiquity remained generally unaccepted for a quarter of a century or more. One of the least prejudiced pioneers in this field of investigation was a Catholic priest, Father J. McEnery, who began digging in Kent's Cavern, Torquay, in 1825 (following excavations carried out in the previous year by antiquarians seeking for evidence that the cave had been used as a Temple of Mithras). Already by 1829 McEnery had found flint implements associated with fossilized bones of rhinoceros and other antediluvian animals below an unbroken floor of stalagmite or dripstone in this cave. To the discoverer these finds demonstrated quite clearly that man had been coeval with animals that had since died out, in some very remote period of time. He did not convince many of those with whom he discussed the finds, but he patiently continued excavating for some fifteen years. While preparing an account of his work for publication he corresponded with Dean Buckland, who expressed the view that McEnery was surely misinterpreting the evidence. Most probably, the Dean argued, the Ancient British people had dug holes for ovens in the stalagmite floor of the cave, and their flint implements had worked down through these into the underlying antediluvian

deposits. McEnery was so discouraged that he abandoned the idea of publishing his manuscript, largely it is said out of deference to Buckland's views. Fortunately his manuscripts were recovered and published posthumously.⁶ Meanwhile precisely similar discoveries were being reported on the Continent.

The first excavations in search of fossil bones in the limestone caves of the Midi (Southern France) had been made by M. Jouannet as early as 1810,⁷ and explorations were continued there in the late eighteen twenties and early thirties by M. Tournal (working mainly in the famous Grotte de Bize in the Aude department) and by several other naturalists. These pioneer investigators found human bones associated with the remains of animals now extinct (at least in that region) such as cave-bear, hyena, reindeer and rhinoceros. Although one of Tournal's collaborators insisted that the human bones found in the Grotte de Bize were in the same chemical condition as the accompanying mammalian bones, there remained doubts about their antiquity in the minds of many because fragments of pottery were said to have occurred in the same layer, suggesting that there had been an intermixture of materials of more than one age. However, Tournal's eventual discovery of extinct animal bones bearing ancient marks of cutting tools appeared to be proof of man's contemporaneity with the extinct fauna at Grotte de Bize (Text-fig. 6), whatever



FIG. 6. Reindeer antler incised by man, from Grotte de Bize (Aude). *After Cartailhac.* Slightly reduced.

the age of the particular human bones found in the deposit might be. Tournal observed that the fossil animal bones could not have been washed into the cave by a catastrophic flood as the diluvialists argued, because many of the remains were disposed in such a way that they could only have been introduced gradually with the enveloping materials in course of successive periods. In other words, Tournal noted that the bone-bearing deposit was stratified.

Stimulated by the discoveries made by the spelaeologists in the Midi, Dr. P. C. Schmerling, anatomist in the University of Liège, began exploring the limestone caves which border the river Meuse not far from that city. His remarkable investigations included reconnaissance of nearly forty caves and extensive excavations in several of them. The majority of the caves had never been explored before, and Schmerling found that their floors were covered by unbroken layers of stalagmite. His excavations revealed underlying deposits of cave-earth, breccia and stream-gravel containing fragmentary skeletons of various extinct animals, including rhinoceros and mammoth, as well as others apparently coeval with them but still extant, such as wolf and wild boar. In four of the caves Schmerling found human remains, and he noted that these were in the same state of preservation as the ancient animal bones with which they were closely associated. His observations on the chemical and physical

condition of the bones are much more precise than those of most of the cave excavators of later years. He pointed out that some of the human bones were found in a stream-worn condition, so there could be no question that they had been intentionally buried in the cave. There could be no doubt, he said, "that the human bones were buried at the same time and by the same causes as the other extinct species".⁸ He also found scattered through these bone-bearing deposits flint implements and worked pieces of bone, leading him to remark: "Even if we had not found human bones in circumstances strongly supporting the assumption that they belonged to the antediluvian period, proof would have been furnished by the worked bones and shaped flints".

In the most famous of the caves explored by Schmerling, the Grotte d'Engis, on the left bank of the Meuse, about eight miles south-west of Liège, he found the remains of three human individuals. They included a child's skull Engis I embedded close to a mammoth tooth, and the skull of an adult (Text-fig. 7) Engis II which was five feet deep in breccia containing bones of horse, reindeer and rhinoceros.



FIG. 7. Fossil human skull (Engis II) found in Grotte d'Engis, Belgium, in 1830. After T. H. Huxley. $\times \frac{1}{2}$ nat. size. Laboratoire de Paléontologie animale de l'Université de Liège.

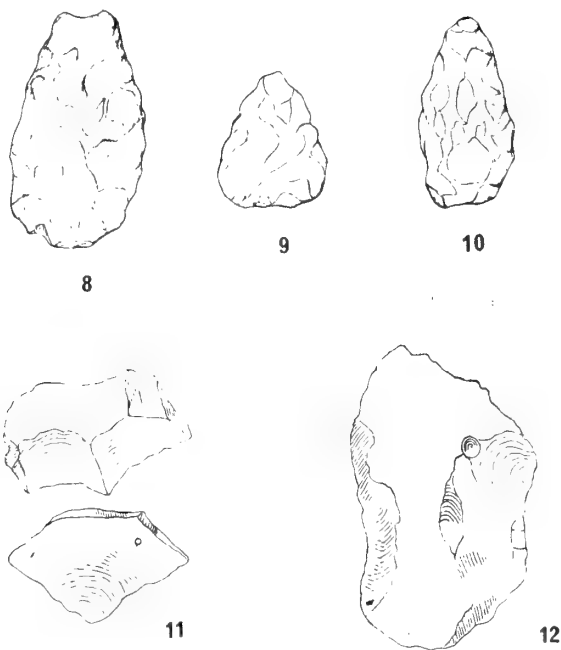
Re-evaluation of the Engis remains⁹ more than a century after their discovery has confirmed the essential correctness of Schmerling's interpretation: they are indeed the first fossil men to be found and recognized as such (see p. 147).

Lyell, like many others, had doubted whether the human bones and the remains of extinct animals in the caves of Gailenreuth and Bize were coeval, but after he had been to see the evidence in Liège he became convinced (as he recorded some years later) that Schmerling "had accumulated ample evidence to prove that Man

had been introduced into the earth at an earlier period than geologists were then willing to believe."¹⁰ In the third edition of his *Principles of Geology* (1834 : 161), Lyell cited Schmerling's findings, but without giving them the weight that he eventually felt they were entitled to.

Although what we might call the battle for the admission of fossil man had really been won by McEnery, Tournal and Schmerling in the years 1829-33, the world at large remained in ignorance until well after 1859 that a great barrier to man's enquiring mind had been removed.

To Boucher de Perthes, Controller of Customs at Abbeville in the second quarter of the last century, goes the credit for having brought to a head the controversy over the question of the antiquity of man. For many years he had made a hobby of collecting antiquities, and in 1836 or 1837 he began to obtain flint axes from the ancient gravels of the Somme. Late in 1838 he read an account of these *haches diluviennes* (Text-figs. 8-10) to the members of the Société d'Emulation d'Abbeville,



FIGS. 8-12. Selection of flints from the Somme gravels figured by Boucher de Perthes, 1847. $\times \frac{1}{4}$ nat. size. Figs. 8-10, *haches diluviennes* (compare Fig. 4). Figs. 11, 12, *industrie antediluvienne*.

but he was not taken seriously, and news of his alleged discoveries did not reach the outside world. Fortunately Boucher de Perthes was not easily daunted ; he quietly continued his researches and in 1846 published the first volume of a work entitled *Antiquités celtiques et antédiluviennes*, proclaiming that the gravels in the suburbs of Abbeville contained stones worked by antediluvian man, and occurring at various depths along with the bones of mammals now extinct. "In spite of their

imperfection", he wrote, "these rude stones prove the existence of man as surely as a whole Louvre would have done". The majority of geologists were frankly scornful of his claims. Darwin once admitted that when he read the work of Boucher de Perthes he thought it was rubbish.¹¹

The controversy which in various places had been simmering for twenty years or more reached boiling point in the eighteen fifties. The scientific world became split into two camps over acceptance of de Perthes' claims. His opponents had the weight of French academic opinion behind them, but their numbers declined after 1854, when Dr. Rigollot, a distinguished physician who had been on their side, was converted to de Perthes' point of view through finding similar flint axes in fossil-bearing gravel at St. Acheul, a suburb of Amiens.

The battle was eventually resolved through British intervention. In the autumn of 1858, the English palaeontologist Hugh Falconer, passing through France on his way to Sicily, paid a visit to Abbeville, and seeing the disputed evidence for himself was very favourably impressed. In the following April, at Falconer's suggestion, the English geologist Joseph Prestwich visited Abbeville and St. Acheul. After examining the collections and inspecting the gravel pits in company with the archaeologist John Evans, he returned to London, and on May 26th read a paper¹² to the Royal Society announcing his acceptance of the claims made by Boucher de Perthes and Rigollot. This announcement, coming from a geologist of such high repute, had a decisive effect on scientific opinion throughout the world. It was all the more effective because at the same time Prestwich was able to announce that excavations then being carried out at Brixham in Devon by William Pengelly, on behalf of the British Association for the Advancement of Science, had completely confirmed the observations of McEnery at Kent's Cavern: flint tools were turning up in association with bones of extinct animals beneath a layer of stalagmite containing remains of mammoth.

Lyell was present at this historic meeting in London, and later that year in the course of an address to the Geological Section of the British Association, meeting in Aberdeen, he said that he was "fully prepared to corroborate the conclusions . . . laid before the Royal Society by Prestwich".

The year 1859 thus stands out as one of the turning points in the history of human thought: the high antiquity of man was established almost simultaneously with the publication of Darwin's book on the *Origin of Species*. Man's antiquity continued to be doubted by scientific diehards for a decade or two. For example the Permanent Secretary of the Academy of Sciences in Paris—a geologist incidentally—remarked in 1863: "I do not believe the Human Race was contemporary with *Elephas primigenius* [mammoth]. Cuvier's theory is born of genius, it is still undemolished"; while even as late as 1875 Victor Meunier's book *Les Ancêtres d'Adam* was suppressed because the publisher feared the displeasure of the Academy.¹³ The same book (edited by A. Thieullen) was published in 1900. As Max Planck once remarked: "A new scientific truth does not triumph by convincing its opponents, but rather because its opponents die, and a new generation grows up that is familiar with it".

SECTION I (Notes)

- ¹ Michèle Mercati died in 1593 ; his book *Metallotheca*, in which ceraunia are figured (p. 243), was published posthumously in Rome, 1717.
- ² FRERE, J. 1800. Account of Flint Weapons discovered at Hoxne in Suffolk (Letter read 22nd June, 1797). *Archaeologia*, London, **13** : 204-205.
- ³ DANIEL, G. E. 1950. *A Hundred Years of Archaeology* : 25. London.
- ⁴ SCHEUCHZER, J. J. 1731. *Physica Sacra*, **1**. Augsburg.
- ⁵ See p. 96 and Daniel, G. E. 1950 : 65.
- ⁶ Published in PENGELLY, W. 1869. The literature of Kent's Cavern, Part II. *Trans. Devon. Ass.*, Plymouth, **3** : 191-482.
- ⁷ CHEYNIER, A. 1936. *Jouannet, grand-père de la Préhistoire*. Brive.
- ⁸ SCHMERLING, P. C. 1833-34. *Recherches sur Ossements fossiles découverts dans les Cavernes de la Province de Liège* : 59. Liège.
- ⁹ TWISSELMANN, F. 1952. In VALLOIS, H. V. & MOVIUS, H. L. Catalogue des Hommes Fossiles. *C. R. XIXe Sess. Congr. Géol. Int.*, Algiers : 37 (95). Note that in Hue, E. 1937. Cranes paléolithiques. *C. R. XIIe Sess. Congr. Préhist. Fr.*, Paris (1936) : 202-204, the accepted usage of Engis I and Engis II has been reversed.
- ¹⁰ LYELL, C. 1863. *The Geological Evidence of the Antiquity of Man* : 70-71. 4th ed. 1873. London.
- ¹¹ DARWIN, F. 1888. *Life and Letters of Charles Darwin*, **3** : 15. London.
- ¹² PRESTWICH, J. 1859. On the occurrence of Flint-implements, associated with the remains of Animals of Extinct species in beds of a late Geological Period, in France at Amiens and Abbeville, and in England at Hoxne. *Proc. Roy. Soc.*, London, **10** : 50-59. A week later, Evans presented the evidence to the Society of Antiquaries.
- ¹³ BOULE, M. 1923. *Fossil Men* : 16. Edinburgh.

II. PERIODS AND ERAS

Since the "Diluvium" was supposed to have been formed in an astonishingly short space of time, "diluvial species" and "antediluvian species" were in theory the same, but in the writings of the diluvialists and uniformitarians alike one detects a growing awareness of a sequence of periods. Thus Boucher de Perthes described the flint axes found in the ancient gravels of the Somme as *diluviennes*, but after discovering some apparently worked flints at greater depths in these gravels he began to distinguish these older and more primitively shaped ones as *antediluviennes*¹ (Text-figs. 11, 12). Then again, John Evans noted in his diary during 1859 : "In this bone cave in Devonshire, now being excavated . . . they say they have found arrowheads among the bones . . . I can hardly believe it. It will make my ancient Britons quite modern if Man is carried back in England to the days when Elephants, Rhinoceroses, Hippopotamuses and Tigers were also inhabitants of the country".²

Prehistory was beginning to stretch out. It is difficult for us to realise today that more than a century ago—say when the present writer's grandfather was at school—there were very few people who had any idea that man had a long unrecorded past. The time prior to history, if it was considered at all, was thought of as a kind of fog without discernible landmarks. In Europe, for example, everything with regard to man that was pre-Roman was lumped together as if belonging to a single period. Indeed, when an eighteenth century antiquary described the famous

pointed flint implement³ found in a trench opposite Black Mary's near Grays Inn Lane, his contemporaries could only imagine that it was the head of a spear used by an ancient Briton in attacking one of the elephants which accompanied the Roman army of Claudius. The process of telescoping the human past, which commonly occurred in the minds of scholars prior to the revolution in thought of 1859, is not unknown of course in untutored minds today, judging by countrymen's comments such as "That was in the time of the Romans, 'fore the railways come. . . ."

The conception that man had an extensive prehistoric past seems to have developed more slowly than the notion of a pre-human, geological past, no doubt because there was a greater emotional resistance to new concepts concerning man himself. One of the most important contributions to dispersing the "prehistoric fog" was made in Denmark where Christian Thomson, having to rearrange the large collection of pre-Roman antiquities in the National Museum, found it necessary in 1819 to postulate three chronologically successive ages : Stone Age, Bronze Age and Iron Age. Finds in excavations soon confirmed the reality of this sequence.

Already during the eighteenth century the idea developed that there had been a long pre-human, geological past, divisible into periods on the basis of the succession of strata observed, for example, in course of mining, digging wells and constructing canals. The broad sequence of stratified rocks had been clearly recognized by the Italian geologist Giovanni Arduino (1713-1795), who proposed that they be divided into three age groups, Primary, Secondary and Tertiary. Practical observations in Britain at about the same time led a civil engineer William Smith ("Father of English Geology") to tabulate the strata in Britain (1799). In 1816 Smith published his great work on *Strata Identified by Organized Fossils*, the foundation of the science of stratigraphy which, as we shall see, has an important part to play in establishing the chronology of early man and his forerunners. These general geological notions did not give rise to such heated controversy as those concerned with the antiquity of man ; they could easily be accommodated to the current beliefs of the diluvialists by presuming that there had been many creations and many deluges. One of Cuvier's students worked out that on the basis of the sequence of fossils there must have been no less than 27 creations.

The strata of the Tertiary group, which included some land and freshwater deposits containing remains of mammals, were subdivided by geologists into a lower group, including the London Clay and the formations in the vicinity of Paris ; a middle group including the sandy formations of Touraine and Bordeaux ; and an upper group comprising all the deposits which were newer than these, including the Diluvium. In course of preparing his *Principles of Geology* (1828-33) Lyell compared the fossil molluscan species in the Tertiary marine formations with those now living, and he found that in the Lower Tertiary not more than $3\frac{1}{2}$ per cent. were identical with those of the present day ;⁴ in the Middle Tertiary, 17 per cent. and in the Upper Tertiary, 35-50 per cent. or even more in the most recent beds. In 1833 he proposed names for these sets of strata and the periods which they represented, as follows : *Eocene* for the Lower Tertiary, meaning *dawn* of recent fauna (from the Greek words *ηως* dawn, *καινος* recent) ; *Miocene*, for the Middle Tertiary, meaning with

fauna containing less recent species than in the succeeding period (from the Greek words for less *μειων* and recent *καινος*) ; and *Pliocene* for the Upper Tertiary, from the Greek words for more *πλειων* and recent. Later,⁵ the uppermost part of the Eocene was separated as *Oligocene*, derived from the Greek words for few *ολιγος* and recent, and the Newer Pliocene was renamed *Pleistocene*, (from the Greek words for most, *πλειστος* and recent).

There was some uncertainty at first as to how much should be included under the term Pleistocene, and this question has been reopened recently ;⁶ but in the third quarter of the nineteenth century the term came into general use to cover the Post-Pliocene deposits commonly called Drift, and formerly known as Diluvium, as distinct from Alluvium.⁷ Thus the Pleistocene included glacial deposits, such as till, or boulder clay, and associated outwash or melt-water sands and gravels, river gravels, lake-beds and cave deposits containing remains of mammals now extinct or living in other regions, such as mammoth, woolly rhinoceros, reindeer and hippopotamus. Pleistocene formations of marine origin were also recognized, their occurrence as raised beaches indicating that relative levels of land and sea have changed repeatedly since the Pliocene period. The fossil molluscan shells in these deposits appeared to be indistinguishable from living species, whereas many of the fossil mammals in contemporaneous deposits laid down on the land were species now extinct. Lyell's classification of geological periods was invented on the basis of shell data, and presumably it was for this reason that he found it unnecessary in the first place to distinguish between Post-Pliocene and Recent ; but his final opinion was expressed in these words :—⁸

“ In the *Recent* we may comprehend those deposits in which not only all the shells but all the fossil mammals are of living species ; in the *Pleistocene* those strata in which the shells being recent, a portion, and often a considerable one, of the accompanying fossil quadrupeds belongs to extinct species ”. He was aware of the arbitrary nature of such classifications, since he added : “ Cases will occur where it may be scarcely possible to draw the line of demarcation between the . . . Pleistocene . . . and the recent deposits : and we must expect these difficulties to increase rather than diminish with every advance in our knowledge. . . ”

It being generally agreed after 1859 or thereabouts that man had existed and was widespread well before the end of the Pleistocene period, which included the Ice Age, the question mainly debated by geologists during the second half of the century concerned the dating of the earliest artifacts and human remains in relation to the glacial deposits. It was widely held for a number of years that relics of man contemporary with Pleistocene mammals, whether in river or lake beds or in cave deposits, were always *post*-glacial. Reading the accounts of these old disputes one cannot help wondering if perhaps the old controversy as to whether man was pre- or post-diluvial was really continuing at the back of the debaters' minds, but with new names for the old ideas.

The realization that there had been an Ice Age during comparatively recent geological times was due primarily to the observations of Swiss amateur naturalists, notably Venetz-Sitten, an engineer who propounded the view in 1829 that glaciers

had formerly extended on to the plains north of the Alps. Another Swiss amateur geologist, Jean de Chapentier, took the young zoologist Louis Agassiz to the Rhône valley in 1836 and demonstrated to him the evidence of earlier glaciation, mainly in the form of ancient moraines. At first Agassiz doubted the sweeping inferences drawn by these amateur geologists, but his own observations and wide reading convinced him that they were right. He went further than they did, and in 1837 he addressed the Société helvétique on the subject of "a great ice period".⁹ He had been impressed by the wide distribution of erratic, or far-travelled, boulders associated with the superficial deposits known as drift in the northern and temperate parts of Europe, Asia and America. During his travels he later noticed rock surfaces that were scratched and polished in a way which Alpine observations had taught him could only be due to the movement of ice masses. After seeing evidence of this kind in the north of England, Scotland and Ireland during the autumn of 1840 Agassiz concluded that "not only glaciers once existed in the British Isles, but large sheets of ice"¹⁰ resembling those now existing in Greenland; and he recognized that these ice sheets had been largely responsible for the formation of the unstratified accumulations of boulder clay or till which were attributed by Buckland and others to the Deluge. It is greatly to Buckland's credit that after Agassiz had shown him glacial agencies at work in the Alps, he recanted his former opinion in these words:¹¹ "Thus the flood that caused the Diluvium which in my 'Bridgewater Treatise' I have put back to the latest of the many Geological Deluges, was probably due to the melting of the Ice".

Although Agassiz communicated a paper to the Geological Society of London in 1840 demonstrating the evidence for the former existence of glaciers in Britain, it was not until Archibald Geikie of the Geological Survey published in 1863 an essay on the Glacial Drift of Scotland¹² that boulder clay became generally accepted as the product of land ice.

When Sir John Lubbock issued his book on *Prehistoric Times* (1865), he proposed that the Stone Age should be divided into: (1) that of the Drift, "when Man shared the possession of Europe with the Mammoth, the Cave Bear and the Woolly-haired Rhinoceros . . ." which he termed the *Palaeolithic* period (from *παλαιος* ancient, and *λιθος* stone) i.e. Old Stone Age; and (2) the Later Stone Age, when the fauna consisted of existing species, and when men used polished stone axes, which he termed the *Neolithic* period (from *νεος* new, and *λιθος* stone).

The river gravels and other freshwater deposits containing palaeolithic flint implements in southern Britain are mainly later than the most widespread boulder clay and the associated melt-water gravels with northern erratics. The famous lake beds with flint hand-axes at Hoxne in Suffolk were observed by Prestwich to *overlie* a thick boulder clay. The gravels containing similar palaeoliths in the Thames Valley were evidently deposited *after* the river had eroded its way through the northern drift. Consequently the opinion that in Britain man was a "post-glacial" immigrant continued to receive support from many geologists during the third quarter of the last century. This view was indeed difficult to refute so long as only a single till or boulder clay had been observed in any one section. Until

the eighteen seventies it was commonly believed that the Glacial epoch was a continuous age of ice, but this was questioned by a few observers, notably the Swiss geologist Morlot (1854), in a paper proposing the division of post-Pliocene time into First Glacial, Diluvian, Second Glacial and Modern epochs.¹³ In the early eighteen seventies a number of observers in various parts of Europe found unmistakable evidence that there had been more than one glaciation. James Geikie, younger brother of Archibald Geikie, collected together all the evidence to show that there had been many changes in climate during the glacial epoch, which he concluded was divisible into a series of alternate cold (*glacial*) and warmer or *interglacial* periods. He assembled the data in favour of this conception in his book *The Great Ice Age and its Relation to the Antiquity of Man* (1874).

An important part of the evidence of climatic change during the Pleistocene is derived from studies of the plant and animal remains in deposits of this period. It was noticed early on that the fossil mammalia in cave deposits and freshwater deposits of Drift age included species of temperate habitat such as bison and grisly bear; species of northern or arctic habitat such as reindeer and musk-ox (also mammoth and woolly rhinoceros); and species of sub-tropical or at least southern habitat such as hippopotamus. The environmental requirements of reindeer and hippopotamus are so extremely different that they cannot have lived contemporaneously in Britain. The requisite habitats are necessarily so far removed from one another that even when Britain was joined to the Continent it was inconceivable, as Geikie pointed out, that hippopotamus and reindeer herds changed places through migrating to and fro with the seasons.

Boyd Dawkins, who considered that seasonal migration might explain the co-mingling of remains of northern and southern species in the same deposit, argued that as the bones of all the species showed the same degree of mineralisation it was not possible to infer that some were derived from older layers. To this Geikie replied:¹⁴ "Mr. Dawkins, I am sure, does not believe that he can distinguish any difference in the state of preservation of a bone say 50,000 years old and that of another say 55,000 years", and yet the time during which arctic forms lived in Britain may not have been separated by any greater interval from the time when a temperate fauna was introduced. That is to say, he believed that two faunas might be represented in the same deposit of river gravel without being precisely contemporary. Up to the time that Geikie was writing, and indeed for some time after, collectors of fossils from gravel pits and even from cave excavations paid little attention to the details of stratification. With the development of more careful methods of collecting and excavation it eventually became evident that many apparent occurrences of northern and southern species in the same layer were simply due to specimens from different but adjacent layers being grouped together by the collectors.

Through observation of cliffs and cuttings in Scotland, Geikie found evidence at several localities of two tills separated by a plane of erosion, and in some places by stratified gravels, sands and peaty muds, indicating a mild interval between two advances of ice. In the Cowdon Burn railway cutting in Renfrewshire, the inter-

calated beds visible in 1868 yielded fossil remains of a temperate fauna, including giant deer, horse and aurochs (*Bos primigenius*), accompanied by seeds of birch and hazel,¹⁵ whereas a till exposed in the Carham sandpit on the Tweed contained tusks of mammoth and antlers of reindeer.¹⁶ At about the same time that these significant observations were being made in Scotland, Searles V. Wood, Jr. and the Rev. J. L. Rome were busy examining the boulder clays and intercalated deposits exposed along the coast of Yorkshire, and correlating them with comparable layers in south-east England ;¹⁷ other geologists were studying the sequence in Lancashire and Cheshire, where Upper and Lower Boulder Clays, with intervening " Middle Sands " were in evidence. Although no one section showed a complete sequence, Geikie was convinced by the evidence of the fossil content of the various layers, and by their relationship to the stages of erosion of the landscape, that there had been three main interglacial periods. By 1877, when the second edition of his book on the *Great Ice Age* was published, he was in a position to synthesize the scattered evidence, and he produced the following conspectus of the climatic oscillations recorded in the Pleistocene deposits in Britain :¹⁸

Last Glacial period : Hessle Boulder Clay ; Upper Boulder Clay of Lancashire. (Followed by valley-moraines in mountain districts.)

Third Interglacial mild period : Hessle Gravel with *Cyrena* [= *Corbicula*] *fluminalis* ; Middle Sands of Lancashire.

Third Glacial period : Purple Clay of Yorkshire ; Lower Boulder Clay of Lancashire.

Second Interglacial mild period : Some intercalated beds ; period of great subaerial erosion.

Second Glacial period : Great Chalky Boulder Clay.

First Interglacial mild period : Sand and rolled gravel above Cromer Clay, with temperate marine molluscan shells.

First Glacial period : Cromer Clay (Till) and Contorted Drift.

Preglacial mild period : Cromer Forest-bed.

Remarkably little advance on this classification has been made in the last seventy years.

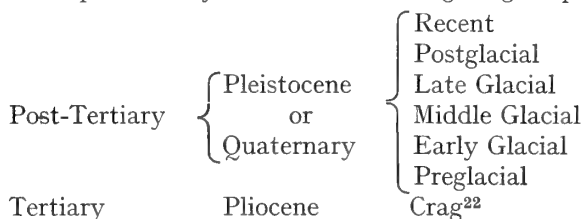
Returning to the question of the geological age of the palaeolithic artifacts found at Hoxne, Geikie pointed out that the boulder clay which underlay them was evidently the Great Chalky Boulder Clay. Thus, far from these implements indicating that man was a post-glacial immigrant, they could equally well be of third or even second interglacial age. In a postscript to the second edition of *The Great Ice Age*¹⁹ Geikie reported that the Fenland geologist, S. B. J. Skertchley, had written to inform him that palaeolithic implements had been found with fossil bones and shells *below* chalky boulder clay near Brandon. In the light of later research one may doubt whether this was the same boulder clay which underlay the Hoxne palaeoliths, but at least there was no longer any doubt that man existed in Britain during an interglacial period.

Geikie paid attention to one line of evidence regarding the antiquity of man which is worth mentioning here as it serves to introduce a method of relative dating

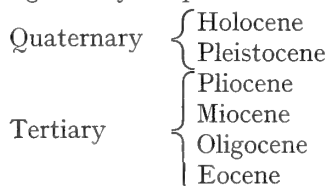
much used in more recent years. He pointed out that the valleys of rivers in Southern England had been excavated 50 or 100 feet since the deposition of gravels containing palaeoliths. The ancient gravels of major rivers, such as the Thames or the Somme, lie on shelves or *terraces* flanking the valleys and marking successive stages in the erosion which gave them their present depth. The occurrence of flint implements of the Hoxne type in the 50 ft. and 100 ft. terraces of the Thames was seen by Geikie as an indication of the immense amount of time that must have elapsed since these tools were manufactured.

In summarizing the evidence for the age of the palaeolithic deposits in Britain Geikie wrote :²⁰ "In short, the palaeolithic deposits dovetail into the glacial drifts. . . . To the last interglacial period . . . we must refer the great bulk of the palaeolithic gravels in the south-east of England. . . . No doubt, however, portions of the ancient tool-bearing gravels, especially in the valley of the Thames . . . may go back to the earlier warm periods of the glacial epoch . . . ; while some may go back to even preglacial ages ".

It is interesting to find that in his classification of the Pleistocene²¹ he was ahead of his time and anticipated modern tendencies, for he included preglacial deposits at the base, and counted the present-day as within the same geological period.



The preponderance of existing species and the presence of man, apparently, throughout Post-Pliocene times led to the idea that the Pleistocene and Recent epochs were best grouped together as a fourth geological era named Quaternary.²³ The equation of Pleistocene with Glacial epoch had left the Recent as equivalent to Post-Glacial ; but to bring it into line with the other period names, Paul Gervais²⁴ proposed in 1850 that it should be called *Holocene* from the Greek words ὅλος whole, and καινός recent). However it was not until the close of the century that the following classification became generally adopted :



By the eighteen sixties there seemed little doubt that man existed early in Quaternary times ; but several questions loomed up as soon as this conclusion was considered in the light of the concept of evolution. Was man's physical form the same in Early and Late Pleistocene times? A small percentage of Recent species of mammalia were in existence at the beginning of the period.²⁵ Perhaps man was

among them—already of the modern species, *Homo sapiens*, at the dawn of the Quaternary era. That was the interpretation that some authorities put on the well-made flint implements reported from relatively early Pleistocene deposits. Were there any fossil remains that confirmed or contradicted this notion? As we shall see, a number of finds of human remains in early Quaternary deposits were reported in the second half of the last century, but there was usually some unresolved doubt, either as to their antiquity or their normality. Was there any evidence in the form of artifacts indicating that man, defined by Benjamin Franklin²⁶ as the “tool-making animal”, existed in Tertiary times?

Beginning with the discovery of some “cut” bones and chipped flints in the so-called Pliocene sands at St. Prest near Chartres,²⁷ a considerable controversy developed over this last question. Some claimed that the specimens found at St. Prest proved the existence of Tertiary Man. Others said that the “cuts” on the bones might be the result of animal gnawings, and that the flints could have been chipped by other natural agencies. Similar flints were reported at about the same time from Tertiary deposits in other parts of France, in Portugal and even in California. Quantities of chipped flints were found by Abbé Louis Bourgeois²⁸ in Lower Miocene deposits at Thenay south of Orleans, and a number of them were examined by a committee of fifteen at the Congress of Anthropology and Prehistoric Archaeology at Brussels in 1872: nine reported in favour of some of these flints being the work of man, five denied that any flint was artificially chipped, and one could not make up his mind.²⁹ Some of the flints were reddened and “crackled”, apparently by fire—although the action of thermal springs could not be ruled out, and in any case fires can be of natural origin.

During the eighteen seventies numerous chipped flints were discovered by J. B. Rames³⁰ in deposits then called Upper Miocene, now regarded as Lower Pliocene, at Puy Courny near Aurillac in the Auvergne, and by Carlos Ribeiro³¹ at Otta near Lisbon. De Mortillet and other archaeologists accepted many of these flints as authentic evidence that a rational being had existed before Quaternary times. Enthusiasm on this subject reached its peak in 1879 when de Mortillet³² argued that as palaeoliths had been made by men differing somewhat from men of the present day, the Tertiary flints must have been flaked by a precursor considerably different from *Homo sapiens*. Carried away by vivid imagination he invented the name *Homosimius* for our Tertiary ape-like precursors; and he went on to attribute the Thenay flints to *Homosimius bourgeoisi*, the Puy Courny flints to *H. ramesi* and the Otta flints to *H. ribeiroi*!

The same author³³ coined the name *eoliths* for the stones in question, that is to say flints whose natural shape was judged to have been slightly altered to make it more useful as a tool. The later part of the Tertiary era was regarded as the *Eolithic Age* (from the Greek words *ηως*, dawn, *λιθος* stone), when naturally shaped stones, it was supposed, were used as implements and occasionally improved. This was the dawn of tool-making which theoretically preceded the Palaeolithic or Old Stone Age coincident with the Pleistocene period.

The enthusiasm for eoliths was infectious. In the eighteen-eighties, Benjamin

Harrison,³⁴ village grocer at Ightham in Kent, whose interest in geology had been aroused in boyhood by reading Lyell's *Elements*, began searching the gravels near the crest of the North Downs, which form the remnant of an ancient plateau. In this gravel he found numerous flints with margins chipped and notched like scrapers and borers. The deposit was regarded by geologists at that time as of Pliocene age. Prestwich showed great interest in Harrison's finds, which were demonstrated at a conversazione of the Royal Society in 1895, and for many years they were widely accepted as the implements of Tertiary Man.

Fortunately for science there are always some sceptics who challenge the current orthodoxy, and the tide of opinion gradually turned against eoliths in the course of the present century, beginning with the discovery, reported by Marcellin Boule³⁵ that lumps of flint, that is to say flint nodules, whirled around in the cement-mixing mills at Nantes, were frequently broken and chipped into eolith-like forms. Whirlpools on river-beds were evidently possible causes of the formation of eoliths ; and there were many other agencies too which may have produced them, notably subsoil pressures. The Abbé Breuil³⁶ found a bed of flints at the base of the Eocene deposits at Clermont (Oise) which had quite evidently been broken and chipped into eolithic forms by the pressures due to movements of the deposits as they settled in adjustment to collapses of the underlying Chalk, which is continually being dissolved by percolating water. In England, Hazzledine Warren made a similar discovery at Grays in Essex, where flint nodules forming the " Bull-head bed " at the junction of the Chalk and the Eocene sands have been fractured and flaked into eolithic forms by these foundering movements.³⁷ Other natural agencies which are known to produce pseudo-artifacts, or naturifacts, include storm waves, cliff-falls, fire, glaciers, frost and soil-creep, particularly of the kind known as solifluxion due to alternate freezing and thawing under periglacial conditions.

It was only to be expected that man's earliest efforts at making tools should be barely distinguishable from the works of Nature. Indeed, one French prehistorian remarked : " Man made one, God made ten thousand. God help the man who can distinguish the one in the ten thousand ". So long as there is *any* doubt about the artificial character of a chipped stone it cannot be regarded as an indication of the presence of man.

Flaked flints have been discovered in large quantities mainly during the present century in and below the Crags of East Anglia. Whether any of these is humanly worked is now regarded as extremely doubtful. Reid Moir, their chief protagonist, always claimed that they were not eoliths, but " Pre-Palaeolithic artifacts ",³⁸ a distinction one would think presupposing some doubt about the former. However, the late Professor Alfred Barnes, who was for many years one of the strongest believers in the humanity of Sub-Crag flakings, showed eventually by application of statistical analysis that they are of the high-angled type characteristic of the work of nature.³⁹ In any case, the Red Crag, Norwich Crag and Weybourne Crag, like the sands of St. Prest, are now regarded as Lower Pleistocene.

Following the archaeological evidence for man's antiquity to its rather dubious limits, it must be admitted that there is really no proof in Europe that humanity

had emerged before the beginning of Quaternary times ; indeed the same is true in Asia and Africa.

We may now more usefully turn to the evidence provided by actual remains of man, considered approximately in their order of discovery and in the light of developing theories and techniques.

SECTION II (Notes)

- ¹ BOUCHER DE PERTHES. 1847. *Antiquités Celtiques et Antédiluviennes*. Paris. Plates 17-23, *Haches diluviennes* ; pls. 27-32, *couteaux diluviennes* ; pls. 50-80, *industries primitives de la période ante-diluviennes*. Many of the flints in these latter plates were in fact "figure-stones" now regarded as natural.
- ² EVANS, J. 1943. *Time and Chance* : 100. London.
- ³ Hand-axe found in 1690, now in the British Museum. Essentially similar to Text-fig. 4.
- ⁴ More detailed studies eventually showed that even in the uppermost division of the Eocene as originally defined, later separated as Oligocene by most authors, not more than one per cent. of the marine mollusca are of Recent species (Davies, A. M. 1934. *Tertiary Faunas*, 2 : 57. London).
- ⁵ Oligocene was proposed by Beyrich, a German specialist on mollusca, in 1839.
- ⁶ Lyell (1833 *Principles of Geology*, 3 : 52. London) used the term "Recent epoch" for the "time which has elapsed since the earth has been tenanted by Man". As thus defined, "Recent" meant Post-Pliocene, and included both the Pleistocene and the Recent as now understood. Later he proposed (Lyell, C. 1839. *Éléments de Géologie* : 621. Paris) the term Pleistocene "as an abbreviation for Newer Pliocene", defined as comprising deposits containing more than 70 per cent. Recent species of mollusca (compared with 40-70 per cent. in the "Older Pliocene"). At the time when he introduced this new term Lyell did not state precisely where its upper and lower boundaries were to be drawn, although by provisionally reclassifying the Norwich Crag as older or true Pliocene he intended the base of the Pleistocene to be above that deposit. It also included some boulder drift (i.e. glacial deposits), but apparently not the valley gravels with flint implements, which were still regarded as Recent. In subsequent works Lyell showed a disinclination to continue using the term Pleistocene, but it had become popular as a result of being adopted in a brilliant essay by the young English geologist Edward Forbes (1846) on the Geological Relations of the existing Fauna and Flora of the British Isles, which stressed the geological and biological significance of the Glacial Epoch. In 1865 (*Elements of Geology*, 6th ed.) Lyell wrote : "I think it best entirely to abstain from the use of the term Pleistocene in this work. . .". He added in a footnote : "If geologists still think it convenient to retain the term Pleistocene, I would recommend them to use it not in the sense originally proposed by me [to mean older Post-Tertiary formations], nor in the somewhat vague manner in which it was applied by Edward Forbes, but in place of Post-Pliocene as this term is defined in the present work". In an accompanying table of strata, the Red Crag, with only 60 per cent. of the mollusca belonging to Recent species, is classified as Older Pliocene, the Norwich Crag, with 89 per cent., is counted as Newer Pliocene, while the Glacial Drift, the Liège and Devon cave deposits, and the Somme gravels, with flint implements and extinct mammalia, are classed as Post-Pliocene. Deposits in which shells and mammalia are all of living species, for example the Danish peats with polished stone and bronze implements, are classed as Recent.
- During the twentieth century the usage of the term Pleistocene has again altered : its base in Britain is now drawn below the Red Crag, while at the upper end some authors would eliminate any formal separation of "Recent" deposits, preferring to regard the age in which we live as a continuation of the Pleistocene (Flint, R. F. 1957. *Glacial and Pleistocene Geology* : 382-384, London).
- ⁷ The term Diluvium was introduced by Gideon Mantell (1822 *Fossils of the South Downs* : 274. London) to mean superficial deposits laid down by agencies no longer operating, particularly

the Biblical Deluge, as distinct from Alluvium, the term for deposits formed by agencies still in force such as existing rivers. In Germany Diluvium is still used as a term synonymous with Pleistocene deposits, but in Britain after the middle of the last century it was replaced by the term *Drift*. The expression "the Drift" originated mainly in connection with the theory that many of the Post-Pliocene deposits, especially those containing erratic or far-travelled boulders, had formed by drifting icebergs at a time when extensive areas of land in the northern hemisphere were submerged (North, F. J. 1943. *Proc. Geol. Ass. Lond.*, **54** : 20). This Drift Theory served as a sort of mental stepping stone between the Diluvial Theory and the Glacial Theory. One group of geologists, the Fluvialists, tried to explain the disposition of almost all superficial deposits by reference to rivers. All these theories had elements of truth in them, and today it is recognized that Pleistocene deposits include products of all the known sedimentary agencies, winds, rain, rivers, floods, lakes, frost, glaciers, floating ice and seas.

- ⁸ LYELL, C. *The Geological Evidence of the Antiquity of Man*. Everyman's Library Ed., edited by R. H. Rastall : 4. 1914. London.
- ⁹ Agassiz commonly receives all or most of the credit for originating the concept of the Ice Age, but this does less than justice to other pioneers and particularly to those colleagues from whom he undoubtedly learnt much of his glaciology, such as Charpentier and Karl Schimper (see de Beer, G. R. 1963. *Charles Darwin* : 75-76, London). Nor should it be forgotten that James Hutton in Edinburgh concluded with remarkable perspicience in 1795 that boulders of Alpine rock noted by de Saussure on the slopes of the Jura mountains had been transported by ice. As regards the idea of continental glaciation, Agassiz was anticipated by A. Bernhardt (1832) who published a paper (*N. Jb. Min. Geol. Paläont.*, Stuttgart, **3** : 257-267) expressing the view that in former times ice had extended overland into Germany from the north polar region. When all is said and done perhaps Agassiz's main contribution in this field was in spreading the new idea, which sounded the death knell of theories based on the Deluge, or on submergence. Thus it was indirectly through Agassiz's visit to Britain in 1840 that Lyell adopted the idea of land-ice as the agency responsible for the formation of certain deposits of till which formerly he attributed to drifting icebergs. For references and fuller discussion of these matters see North, F. J. 1943. Centenary of the Glacial Theory. *Proc. Geol. Ass. Lond.*, **54** : 1-28.
- ¹⁰ AGASSIZ, L. 1840. On glaciers, and the evidence of their having once existed in Scotland, Ireland and England. *Proc. Geol. Soc. Lond.*, **3** : 327-332.
- ¹¹ SOLLAS, W. J. 1905. *The Age of the Earth and Other Essays* : 247. London.
- ¹² GEIKIE, A. 1863. The Phenomena of the Glacial Drift of Scotland. *Trans. Geol. Soc. Glasgow*, **1** : 2.
- ¹³ MORLOT, A. 1854. Notice sur le Quaternaire en Suisse. *Bull. Soc. vaud. Sci. nat.*, Lausanne, **4** : 41-45.
- ¹⁴ GEIKIE, J. 1877. *The Great Ice Age* : 523. 2nd ed. London.
- ¹⁵ GEIKIE, J. 1877. *The Great Ice Age* : 127. 2nd ed. London. This author first formulated the concept of an interglacial period in 1871 (*Geol. Mag.*, London, **8** : 545-553). Earlier writers in Britain had used the term interglacial, but only in the sense of *intraglacial*.
- ¹⁶ GEIKIE, J. 1877. *The Great Ice Age* : 129. 2nd ed. London.
- ¹⁷ WOOD, S. V. & ROME, J. L. 1868. On the Glacial and Postglacial Structure of Lincolnshire and South-east Yorkshire. *Quart. J. Geol. Soc. Lond.*, **24** : 146-184.
- ¹⁸ GEIKIE, J. 1877. *The Great Ice Age* : 393. 2nd ed. London. The only fundamental error in this author's conception of the Pleistocene was his belief that Britain was submerged during the "last Interglacial" period to a depth of up to 1,300 feet. This misconception was based on the occurrence of shelly drift at that height, for instance on Moel Tryfaen in Wales. Subsequently it was shown that such deposition was the result of coastal ice being thrust up under pressure from the main ice-caps, whose heads were at still greater elevations.
- ¹⁹ GEIKIE, J. 1877 : 565.
- ²⁰ GEIKIE, J. 1877 : 531-532.

- ²¹ GEIKIE, J. 1877. *The Great Ice Age* : 566.
- ²² *Crag* is a Suffolk dialect term for the shelly marine sands of Upper Pliocene and Lower Pleistocene age which occur extensively in East Anglia. The term probably came from the Celtic word *cregga* meaning a shell (Arkell, W. J. & Tomkief, S. I. 1953. *English Rock Names* : 31. Oxford).
- ²³ The term Quaternary was introduced by Desnoyers in 1829 (*Ann. Sci. nat.*, Paris, **16** : 193), but it was first used by Reboul on a faunal basis to mean Post-Pliocene deposits of prehistoric and historic periods (1833 *Géologie de la période Quaternaire*. Paris).
- ²⁴ *Holocene* was first proposed in 1850 by Paul Gervais for post-Pleistocene deposits (*Mém. Acad. Montpellier (Sci.)* **1** : 413) ; but it was not generally adopted until the end of the century when the term was independently proposed by B. B. Woodward (1897 *Essex Nat.*, Buckhurst Hill, **10** : 92). The late Mr. A. S. Kennard told the present writer that the term was suggested by an intelligent working man who wrote to Dr. Henry Woodward pointing out that such a term seemed to be needed ; and Dr. Woodward passed the letter on to B. B. Woodward who decided to introduce it in his next paper.
- ²⁵ For example *Hippopotamus amphibius*.
- ²⁶ Quoted in Boswell's *Life of Johnson* under 7 April, 1778.
- ²⁷ DESNOYERS, J. P. F. S. 1868. *C. R. Acad. Sci. Paris*, **1868** : 1077, 1082, 1199 ; BOURGEOIS, L. 1867. *C. R. Acad. Sci. Paris*, **1867** : 47.
- ²⁸ BOURGEOIS, L. 1872. Sur les Silex considérés comme portant les marques d'un travail humain découverts dans le terrain Miocène de Thenay. *C. R. Congr. Anthropol.*, Bruxelles, 81-92. The deposit belongs to the Aquitanian stage, classified by some authorities as Upper Oligocene, but now generally placed in the Lower Miocene.
- ²⁹ DANIEL, G. E. 1950. *A Hundred Years of Archaeology*.
- ³⁰ RAMES, J. B. 1884. *Géologie du Puy Courmy*. In *Matériaux pour l'Histoire naturelle et primitive de l'Homme* : 399-403.
- ³¹ RIBEIRO, C. 1872. *C. R. Congr. Anthropol.*, Bruxelles, **1872** : 95.
- ³² MORTILLET, G. DE. 1879. *Rev. anthrop.*, Paris, **1879** : 117.
- ³³ MORTILLET, G. DE. 1883. *Le Préhistoire* : 18. Paris.
- ³⁴ HARRISON, E. R. 1928. *Harrison of Ightham* : 133, 292. Oxford.
- ³⁵ BOULE, M. 1905. L'Origine des Eolithes. *Anthropologie*, Paris, **16** : 257-267.
- ³⁶ BREUIL, H. 1910. Sur la presence d'Eolithes à la base de l'Éocène Parisien. *Anthropologie*, Paris, **21** : 385-408.
- ³⁷ WARREN, S. H. 1920. A Natural "Eolith" Factory beneath the Thanet Sand. *Quart. J. Geol. Soc. Lond.*, **76** : 238-253.
- ³⁸ MOIR, J. R. 1927. *The Antiquity of Man in East Anglia* : 35. Cambridge.
- ³⁹ BARNES, A. S. 1939. The differences between natural and human flaking on prehistoric flint implements. *Amer. Anthropol.*, Lancaster, **41** : 99-112.

III. EARLY ATTEMPTS AT DATING : AURIGNAC, NEANDERTHAL AND MOULIN-QUIGNON

We have seen that early in the last century human skeletal remains were found in Pleistocene cave deposits at a number of localities in Europe, and that some were eventually accepted as contemporaneous with the associated extinct fauna, the most notable examples being the Paviland skeleton (1823) and the Engis skulls (1830).

In 1852 a labourer mending a road across a hillside at Aurignac in the Haute Garonne province of southern France noticed a rabbit-hole, and reaching into it as far as he could, perhaps hoping to catch a rabbit, he drew out a human limb-bone.

His curiosity aroused, he dug a trench into the hillside and revealed a cave whose mouth had been closed by a vertical slab of limestone, and behind which there was a cavity almost filled with human bones representing seventeen skeletons of almost all ages. The mayor of Aurignac decreed that all the human bones must be reburied in the local Christian cemetery. The labourer's trench had also brought to light some bones of extinct animals and bone carvings. When Edouard Lartet, a lawyer who had turned to palaeontology and prehistory, heard of these finds eight years later he visited Aurignac and began digging into the deposits on the slope below the cave. He discovered a number of hearths and a fair number of flint implements, bone points and worked pieces of reindeer antler, together with bones of cave-bear, mammoth, woolly rhinoceros and bison (Text-fig. 13).

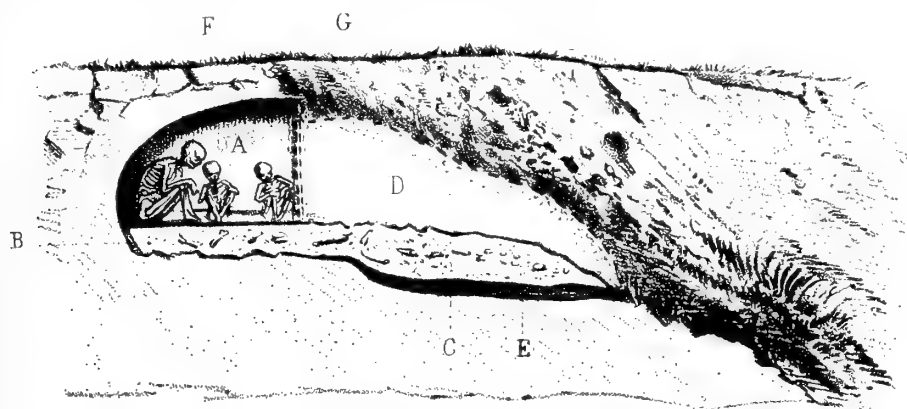


FIG. 13. The cave at Aurignac as figured by Edouard Lartet. A, Burial chamber, presumed Neolithic; B, Upper Palaeolithic (Aurignacian) occupation deposit.

Lartet formed the opinion that the human skeletons and the glacial fauna at Aurignac were contemporaneous,¹ but this view was disputed by other investigators. The final conclusion was that the human skeletons represented a collective burial of the Neolithic period on top of a disturbed cave deposit of Upper Palaeolithic age.² Lartet found some detached human bones mixed with bones of glacial mammals in the substratum of the burial chamber. At his request, chemical analysis was made of one of the human bones, as well as of bones of associated rhinoceros and other extinct animals. All the analysed bones proved to contain the same percentage of nitrogen, that is to say they had all lost about the same proportion of gelatine. This is of historic interest because it was the first application of what has become known more recently as the collagen or *nitrogen test* for the relative dating of bones. The result was not considered conclusive by Lartet's critics because of the possibility that the loss of gelatine in ageing bones only proceeds so far and no further so long as the bone is enveloped in matrix. As Lyell said:³ "... had the human skeletons been found to contain more gelatine than those of the extinct mammalia, it would have shown they were the more modern of the two". The fact that they contained the same amount was inconclusive.

Up to the middle of the last century none of the human remains which had been found associated with Pleistocene mammals showed features clearly distinguishing them from men living today. The anatomist George Busk considered that the well authenticated adult Engis skull, for example, although narrow in the forehead might be matched among skulls of individuals of the European race, while Thomas Huxley showed by measurement that it fell well within the range of variation of modern Australian skulls.

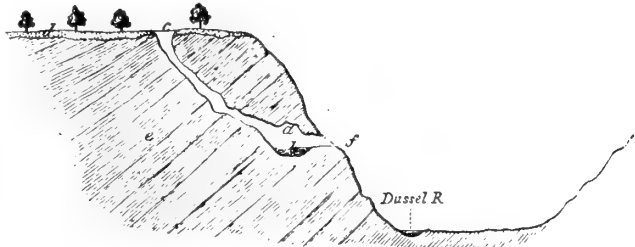


FIG. 14. Section of the Neanderthal Cave near Düsseldorf. *After Lyell.* (a) Cavern 60 feet above the Dussel, and 100 feet below the surface of the country at c ; (b) Loam covering the floor of the cave near the bottom of which the human skeleton was found ; (b, c) Rent connecting the cave with the upper surface of the country ; (d) Superficial sandy loam ; (e) Devonian limestone ; (f) Terrace, or ledge of rock.

In August 1856 a remarkable fossil human skull with associated limb-bones came to light in Germany. The bones were in a muddy cave deposit exposed during the quarrying of limestone in the ravine known as Neanderthal near Düsseldorf in the Rhineland⁴ (Text-fig. 14). The remains were saved from destruction by Dr. C. Fuhlrott and described in the following year by Professor H. Schaaffhausen of Bonn. After comparing the Neanderthal cranium (Text-fig. 15) with many others, ancient and modern, the latter concluded:⁵ " But the human bones and cranium from the Neanderthal exceed all the rest in those peculiarities of conforma-



FIG. 15. Fossil human skull-cap found at Neanderthal in 1856. *After T. H. Huxley.* $\times \frac{1}{2}$ nat. size. Rheinisches Landesmuseum, Bonn.

tion which lead to the conclusion of their belonging to a barbarous and savage race". And further, he thought that they might "be regarded as the most ancient memorial of the early inhabitants of Europe".

Great interest was eventually aroused by this skull, particularly in view of its possible bearing on the animal origins of man, a subject which was soon to be much in the minds of those who realized the full implication of Darwin's *Origin of Species* published in 1859. The German anthropologist Virchow had declared that the skull was that of a pathological idiot. Huxley on the other hand, after making a detailed study of a cast of the skull which had been sent to him, accepted it as human and as undiseased. He wrote:⁶ "In truth the Neanderthal cranium has most extraordinary characters". He commented especially on its vast development of superciliary (eyebrow) ridges, extensive frontal sinuses, retreating forehead, very low vault and flat protruding occipital region. "Under whatever aspect we view this cranium . . . we meet with ape-like characters, stamping it as the most pithecoïd of human crania yet discovered". But having said this he proceeded to stress the contrary indications. The cranial capacity was estimated to have been about 75 cubic inches (c. 1230 cc.), a figure almost identical with that quoted as the average cranial capacity of Hottentots. Moreover, after comparing it with a rugged male skull from the Neolithic tumulus at Borreby in Denmark, and with Australian aboriginal skulls, he concluded that the Neanderthal cranium was not an isolated type intermediate between apes and man, but rather "an extreme term in a series leading gradually from it to the highest and best developed of human crania".

Huxley also pointed out that the dimensions of the other bones of the skeleton showed that both in absolute height and relative proportions the limbs of Neanderthal Man were quite like those of a modern European of medium stature. It was true, he said, the bones were stouter, but "The Patagonians, exposed without shelter or protection to a climate possibly not very dissimilar from that of Europe at the time during which the Neanderthal Men lived, are remarkable for the stoutness of their limb bones".

A critical question naturally was the antiquity of the Neanderthal skeleton. No fossil mammalian remains were reported in association, although the canine of a bear was found in a lateral branch of the same cave,⁷ and fossils of the Mammoth fauna occurred in a similar cave only 133 paces away.⁸ Schaaffhausen reported that the bones of the Neanderthal skeleton "adhere strongly to the tongue, although as proved by the use of hydrochloric acid, the greater part of the cartilage is still retained in them, which appears, however, to have undergone that transformation into gelatine which has been observed by v. Bibra in fossil bones". [This early recognition of denatured collagen in fossil bone is of considerable interest.]⁹ "The surface of all the bones is in many places covered with minute black specks, which, more especially under a lens, are seen to be formed of very delicate *dendrites*. . . . They consist of a ferruginous compound, and from their black colour may be supposed to contain manganese" (Text-fig. 16).

It had long been supposed that the presence of dendrites on a bone was a mark of distinction between truly fossilized, Pleistocene, bones and those which had been

mixed with a Pleistocene deposit at a recent date. However, Professor von Meyer told Schaaffhausen that he had seen dendrites of undoubtedly recent origin (on paper!), and furthermore, that he possessed a dog's skull of Roman age which was in no way distinguishable from fossil bones from Frankish caves, presenting the same colour and adhering to the tongue—"so this character also, which at a former meeting of German naturalists in Bonn, gave rise to amusing scenes between Buckland and Schmerling, is no longer of any value".¹⁰



FIG. 16. Dendrite on bone. Enlarged.

So long as no other skulls of the same type were known, and so long as there was no direct evidence of its antiquity, views as to the date of the Neanderthal Man naturally varied widely. Professor F. Mayer of Bonn regarded the skeleton as probably that of a "rickety Mongolian Cossack" who, on his way through Germany towards France in 1814, had crept into the cave and died.¹¹ Schaaffhausen on the other hand was convinced that the man "belonged to a period antecedent to the time of the Celts and Germans", perhaps "derived from one of the wild races of Northwestern Europe, spoken of by the Latin writers", but doubtless "traceable to a period at which the latest animals of the diluvium still existed".

Lyell thought that von Meyer had overdone the discrediting of the usually accepted criteria of fossilization. The profuse dendrites on the outer and inner surfaces of the cranium, together with the fact that the texture of the bone agreed with that of typical Pleistocene fossils, led him to conclude: "On the whole I think it probable that this fossil may be of about the same age as those found by Schmerling in the Liège caverns . . .".

While Huxley regarded the Neanderthal skull as representing no more than an extreme variant of *Homo sapiens*, William King, anatomist at Queen's College, Galway, considered that the skull was so eminently ape-like that he doubted whether it could be grouped with existing man, and argued that it was better treated at least as a distinct species.¹² At the meeting of the British Association for the Advancement of Science, held in Newcastle in 1863, he proposed the name *Homo neanderthalensis*, and this was published in the following year.

The idea that the world had at one time been peopled by men of a species now extinct was new, and although there has been to some extent a swing back to Huxley's interpretation of Neanderthal Man during recent years, nevertheless King's recognition that this was a type of man who flourished during the Pleistocene period and has since died out was in fact a bold one and contributed considerably to the development of anthropological thought.

In the following year, at the meeting of the British Association in Bath, George Busk,¹³ Professor of Anatomy at the Royal College of Surgeons, gave an account

of another fossil skull (Plate 1), which had recently been sent to him from Gibraltar by Captain Brome, Governor of the Military Prison there.¹⁴ The skull had been discovered during work in Forbes Quarry on the North Front, and presented to the Gibraltar Scientific Society by Lieutenant Flint of the Royal Artillery on March 3rd 1848, but the news had not been published. Busk recognized that this skull was of the same type as the Neanderthal skull, but it was more complete, with face, upper jaw and teeth preserved. The palaeontologist Hugh Falconer had also examined it, and in a letter which he had written to Busk before the British Association meeting (1864) he proposed the name *Homo calpicus* (after Calpé, the ancient name of Gibraltar) for the extinct species of mankind which it represented.¹⁵ This name was not published at the time but since the skull was identifiable with that of Neanderthal, the name proposed by King which was already published would have had priority.

Although the Gibraltar skull was in fact the second¹⁶ example of *Homo neanderthalensis* to be made known to the scientific world, full confirmation that King had been right in regarding the Neanderthal Man as representative of a distinct Pleistocene branch of mankind did not come until 1886 when two skeletons with skulls of the same remarkable form were discovered in cave deposits at Spy near Namur in Belgium.¹⁷

From the dating point of view the importance of the discovery at Spy lay in the fact that the human remains were excavated with scientific precision. Thus it was certain that they were found in a layer containing bones of woolly rhinoceros and mammoth, and were associated with Palaeolithic implements of a well-defined type (p. 130), termed Mousterian, known to be later than the hand-axe industries, found for instance in the Somme gravels at Abbeville and St. Acheul, which were later termed Chellean.

The problem which now began to emerge was whether *Homo neanderthalensis* had preceded or existed alongside *Homo sapiens*. Closely linked with this problem was the question of the physical character of the men who had made the Chellean hand-axes. There had been a fair number of discoveries of fossil or apparently fossil remains of *Homo sapiens*, some in deposits with Upper Pleistocene fauna (including mammoth, woolly rhinoceros and reindeer), which might be contemporary or more probably later than the Neanderthal species, for example in the Liège caves ; but others, much more puzzling, were in considerably older deposits.

For many years Boucher de Perthes had cherished the hope of finding bones of the men who made the flint hand-axes (*haches*) which he had been the first to recognize as human artifacts in the terrace gravels of the Somme. It is said¹⁸ that he had offered 200 francs reward to any of the gravel diggers who should find fossil human bones with these early flint tools. As the men only earned two francs a week this was a large reward. He was now seventy-five years old. How much longer would he have to wait ? On March 23rd, 1863, one of the diggers or *terrassiers* brought to him two flint *haches*, and what appeared to be a scrap of fossil bone covered by dark sandy deposit, which the man said had been found near the bottom of the gravel which was then being dug in the Moulin-Quignon pit near Abbeville. On

removing its sandy matrix, Boucher de Perthes found that the "fossil bone" was actually a human tooth. Five days later he was called to the same gravel pit, where he was shown a fragment of bone projecting from a black seam of sandy gravel (*couche noire*), about 15 feet below the surface, close to the base of the section. On removing this fragment with his own hands, he found it was the left half of a human jawbone, or mandible, with the second molar still in place. The discovery was announced in a local newspaper on April 9th, and Prestwich, Falconer and Evans who happened to be in France at the time decided to visit the site in the following week. Evans and Prestwich arrived first, and their suspicions were immediately aroused. They were convinced that the *haches* from the black seam of gravel which had yielded the jawbone were modern forgeries. Falconer went later, and his first impression of the jaw was favourable to its being of fossil antiquity, but after returning to London, as soon as he had had an opportunity to scrutinize the material he had taken back with him, doubts arose in his mind. The axes looked spurious, and the isolated molar tooth which he had been allowed to borrow and to saw in half evidently contained a great deal of gelatine. On April 21st, he wrote to Edouard Lartet, who had possession of the jaw, saying that Evans, Prestwich, Busk, and he were opposed to the authenticity of the isolated molar and the *haches*. Meanwhile news of the discovery of the jaw, assumed to be authentic, had been communicated to the Royal Society in London, and the Academy of Sciences in Paris. On April 25th *The Times* published a letter from Falconer strongly questioning the authenticity of the *haches* and the jawbone. This cleavage of opinion resulted in the French *savants* promptly inviting their English challengers to meet them at a conference in Paris, beginning on May 9th. The conference lasted for five days. The report on its proceedings¹⁹ and the notes prepared by Falconer in the course of these deliberations are still of unusual interest (Text-fig. 17).



FIG. 17. Discussion on the Moulin-Quignon jaw at the Academy of Sciences, Paris, After *L'Illustration du Midi*, 1863.

Three lines of evidence were considered : the intrinsic evidence of the jawbone ; the intrinsic evidence of the *haches* ; and the extrinsic evidence, that is to say the geology of the site and the circumstances of the discovery.



FIG. 18. Moulin-Quignon jaw. *After Delesse*. Nat. size. Musée de l'Homme, Paris.

The form or morphology of the jaw was not discussed, but clearly it conformed with that of *Homo sapiens* (Text-fig. 18). When the question of whether the condition of the jawbone was consistent with fossil antiquity came up for consideration, Busk was allowed to saw it in half, just in front of the solitary molar, so that the section included a portion of the roots. Falconer pointed out the many features which were against the jaw being contemporary with the black mangano-ferruginous gravel in which it was said to have lain. It showed no abrasion or appearance of having been rolled on the river bed, the thin coronoid process was as perfectly preserved as in a Recent jawbone, while the black sandy coating washed off with the greatest ease when the specimen was brushed in warm water. There were no dendrites on the bone, which therefore differed conspicuously from bones of undoubted fossil antiquity in the Somme gravels. The true fossil bones also contrasted strongly with the Moulin-Quignon jaw in having lost most of their gelatine. On sawing, the jawbone proved to be hard and firm, and the "fresh section afforded a distinct odour of sawn bone". Internally the bone structure was free from any kind of mineral impregnation. The dental nerve canal contained fine grey sand, but without any speck of the black matter which was so conspicuous in the enveloping matrix. The section of the root of the molar "showed that the dentine, so far as it was exposed, was perfectly white, full of gelatine, and in no respect different in appearance from that of a Recent tooth". [These words were unwittingly echoed when the notorious Piltdown jawbone was being re-described in 1950.] The body of the molar in the jaw showed carious decay, which we now know to have been rare in Palaeolithic people.

The members of the conference heard evidence that in some circumstances fossil bones and teeth retain a considerable proportion of their organic matter, or gelatine. Two teeth of the extinct cave-hyaena from Pleistocene deposits in Auvers were produced by Monsieur Delesse in support of this point. But Busk, while admitting that the jawbone might be of considerable age, said that he was convinced that it was not of high antiquity, for it "presented no character which may not be found in cemetery bones". He compared the jaw with a specimen from a Gallo-Roman cemetery near Amiens, from which it only differed in being slightly less altered, and in having the sand grains in the dental canal. All these comparisons were qualitative rather than quantitative. "One important part of the intrinsic evidence", Falconer wrote,²⁰ "still remained to be determined, namely the chemical analysis of the bone, but the conference was too pressed for time to wait for it".

The best part of three days were devoted to considering the intrinsic evidence of the *haches* or hand-axes recorded from the *couche noire*. These differed from the undoubtedly genuine hand-axes found in the Somme gravels in a number of important respects. According to Falconer the facets were deeper and narrower, corresponding with iron-struck, rather than with stone-struck flakes, and were disposed with a greater sameness of pattern as though produced by one or two hands. The ridges between the flake facets were higher and sharper. The surfaces had the dullness of recent fracture, rather than the gleam of ancient flint artifacts from gravel, and they lacked dendrites (Text-fig. 16) and all trace of patina or ferruginous staining. Some had a ferruginous incrustation, but this proved to be quite superficial and easily washed off.

The conference proceeded to Abbeville on May 12, and in the Moulin-Quignon pit watched a large party of workmen digging in the gravel in search of implements. Five *haches* "were yielded during the operations of the day; and in no case was any circumstance observed or noted which would justify the opinion that they had been fraudulently introduced".²¹ Four of these worked flints were later examined in England, and although one showed the characteristics of a genuine palaeolith, the other three bore all the signs of recent fabrication. However, the French members of the conference were satisfied that Boucher de Perthes was not being deceived. They admitted the difficulty of distinguishing the genuine from the counterfeit in some instances, but they argued that if the position of an axe in a deposit was unquestionable, the axe itself must be accepted as genuine.

As regards the extrinsic evidence, one of the geologists who visited the pit on May 12th made a suggestion which at first seemed to offer a happier solution than either doubtfully accepting the jawbone as Pleistocene, or regarding it as a fraudulent intrusion. He pointed out that there were deep "sand pipes" extending throughout the whole thickness of the ancient gravels in the Moulin-Quignon pit, one close to where the jaw is said to have been found, and the deposits in these pipes might be of Post-Pleistocene age. Possibly the jawbone had in reality come from such a deposit. However, the majority of those who inspected the section considered that the *couche noire* which yielded the jawbone unquestionably belonged to the high-level terrace of the Somme which contained the early hand-

axes. Chemical tests on the material of the bed showed that it contained no humic or other organic matter.

The following conclusions were reached on the last day of the conference, and forwarded to the Academy of Sciences for consideration at its session on May 18th, 1863 :—

- (1) The jawbone was *not* fraudulently introduced into the Moulin-Quignon pit.
- (2) All the members present, with the exception of Falconer and Busk, incline to think that the jaw-bone is contemporaneous with the *couche noire* in which it was found.
- (3) The *haches* presented as having been found in the lower part of the section in the Moulin-Quignon pit are for the most part authentic.

The English members of the conference and their colleagues at home were far from satisfied. John Evans wrote a letter to the *Athenaeum* of June 6th protesting that all the *haches* recently found in the Moulin-Quignon pit were in his opinion spurious.²² He also wrote to Boucher de Perthes with the request that one of his most trusted workers, Mr. H. Keeping, should be allowed to watch the excavations in progress in this pit for one week. Boucher de Perthes agreed. At the end of the week's vigil, Keeping had all the evidence required to prove that *haches* were being fraudulently planted in the gravels.²³ In a letter to the *Athenaeum* of July 4th, 1863, Evans described Keeping's report and said (p. 20) :

" I sincerely hope that the human jaw from Moulin-Quignon may from this time forward be consigned to oblivion. *Requiescat in pace!*" But he added in conclusion that these particular finds being proved fraudulent " has nothing whatever to do with the evidence afforded of the antiquity of Man by his work discovered in the drift . . . the general rule holds good, that the existence of counterfeits presupposes the existence of genuine originals ".

In the following year a second jaw-bone and other human bones were found in the Moulin-Quignon pit, and were accepted by some French authorities as confirmation of the authenticity of the original find ; but by the scientific world at large they were simply taken as an indication that the *terrassiers* had again succeeded in their trickery. The Moulin-Quignon jaw received its *coup de grâce* in 1950 when it was submitted to the fluorine test.

Subsequently to the Paris conference the anatomical form or morphology of the Moulin-Quignon specimen was attentively studied by the French anthropologist Prüner-Bey,²⁵ who found that it corresponded closely to a mandible of a late prehistoric skull from Switzerland, and he concluded that the Moulin-Quignon specimen could well have belonged to a brachycephalic individual " of the stone age ", by which he meant in this case Neolithic.

The fact that the controversial jaw was patently indistinguishable from jaws of modern *Homo sapiens* had almost been lost sight of in the heat of the discussions on its age and authenticity. However, this aspect of the matter must have been brought sharply to mind when, a year or so later, a fossilized lower jaw obviously differing somewhat from the modern type, and perhaps referable to the Neanderthal species, was found with glacial fauna in the cave called Trou de la Naulette, near Dinant.

It was described by Prüner-Bey.²⁵ While adding to knowledge, it did not help towards solving the problem of human origins.

In his famous essay on the Engis and Neanderthal skulls, Huxley²⁶ said that these fossil remains of man did not seem to "take us appreciably nearer to that lower pithecoïd form, by the modification of which he [man] has, probably, become what he is". Indeed he thought that judging by their flint "axes" and "knives" the earliest men of the glacial period were probably not inferior to the lowest savages of our own time. He asked: "Where, then, must we look for primæval Man? Was the oldest *Homo sapiens* Pliocene or Miocene, or yet more ancient? In still older strata do the fossilized bones of an Ape more anthropoid, or a Man more pithecoïd, than any yet known await the researches of some unborn palæontologist?"

SECTION III (Notes)

- ¹ LARTET, E. 1861. Nouvelles recherches sur la Coexistence de l'Homme et des grands Mammifères fossiles. *Ann. Sci. nat. Paris* (4, Zool.) **15** : 177-253, pls. 1-13.
- ² VALLOIS, H. V. 1953. In Catalogue des Hommes Fossiles. *C. R. XIXe Sess. Congr. géol. int.*, Algiers, 1952 : 162.
- ³ LYELL, C. 1873. *The Geological Evidence of the Antiquity of Man* : 129. 4th ed. London.
- ⁴ CAMPBELL, B. 1956. The Centenary of Neanderthal Man. *Man*, London, **56** : 156-158, 1 fig.
- ⁵ SCHAAFFHAUSEN, H. 1861. On the Crania of the Most Ancient Races of Man, translated by G. Busk. *Nat. Hist. Rev.*, London (n.s.) **1** : 155-172.
- ⁶ HUXLEY, T. H. 1863. *Evidence as to Man's Place in Nature* : 142. London.
- ⁷ LYELL, C. 1873. *The Geological Evidence of the Antiquity of Man* : 82. 4th ed. London.
- ⁸ SOLLAS, W. H. 1924. *Ancient Hunters* : 229. 3rd ed. London.
- ⁹ OAKLEY, K. P. 1963. Analytical Methods of Dating Bone. In Brothwell, D. R. & Higgs, E. S. *Science in Archaeology* : 24-34. London.
- ¹⁰ HUXLEY, T. H. 1863. *Evidence as to Man's Place in Nature* : 135. London.
- ¹¹ MAYER, F. 1864. Über die fossilen Überreste eines menschlichen Schädels und Skeletes in einer Felsenhöhle des Düssel- oder Neander-Thales. *Arch. Anat. Physiol.*, Lpz., **1864** : 1-26.
- ¹² KING, W. 1864. On the Neanderthal Skull, or Reasons for believing it to belong to the Clydian Period, and to a Species different from that represented by Man. *Rep. Brit. Ass.* London, **1863**, Abstracts : 81.

By "Clydian Period" King meant the time represented by the marine clays containing arctic species of mollusca, which occur extensively in the Clyde district of Scotland. These beds were referred by James Geikie (1877) to the "Last Glacial Period". Modern work has confirmed that Neanderthal Man attained his maximum development during the early part of the Last or Würm glaciation (see pp. 130-131).

The specific name *Homo neanderthalensis* dates from the publication of King's second paper (1864. The Reputed Fossil Man of Neanderthal. *Quart. J. Sci.*, London, **1** : 88-97) which gives an indication of some of the distinctive characteristics.

- ¹³ BUSK, G. 1865. On a very Ancient Human Cranium from Gibraltar. *Rep. Brit. Ass.*, London, **1864**, Abstracts : 91-92.

Although no extinct mammalia were recorded in association with the skull, Busk remarked that the condition of the bone showed it was of great antiquity.

- ¹⁴ CAMPBELL, B. 1956. The Centenary of Neanderthal Man. *Man*, London, **56** : 156, 171-173.
- ¹⁵ KEITH, A. 1911. The Early History of the Gibraltar Skull. *Nature*, Lond., **87** : 313.

It is interesting that Falconer in 1864 referred to the Gibraltar skull in these terms: "I do not regard this *priscan pithecoïd man* as the 'missing link' so to speak. It is a case

- of a very low type of humanity—very low and savage, and of extreme antiquity—but still man, and not a halfway step between man and monkey". (*Palaeontological Memoirs and Notes*, 2 : 561, footnote. Ed. C. Murchison, London, 1868).
- ¹⁶ Engis I child's skull discovered in 1830 and published by Schmerling in 1833 (*Recherches sur les ossements fossiles découvertes dans les cavernes de la province de Liège* : 62. Liège) ultimately proved to be Neanderthal, but was not recognized as such until 1936 (Fraipont, C. *Les Hommes fossiles d'Engis*. *Arch. Inst. Paléont. hum.*, 16. Paris).
- ¹⁷ FRAIPONT, J. & LOHEST, M. 1887. *Recherches ethnographiques sur les ossements humains découverts dans les dépôts quaternaires d'une grotte à Spy et détermination de leur âge géologique*. *Arch. Biol. Paris*, 7 : 587-757.
- ¹⁸ VAYSON DE PRADENNE, A. 1932. *Les Fraudes en Archéologie Préhistorique* : 65-101. Paris. See also Cole, S. 1955. *Counterfeit* : 121-127. London.
- ¹⁹ DELESSE, A. 1863. *La Mâchoire Humaine de Moulin de Quignon*. *Mém. Soc. Anthropol. Paris*, 2 : 37-68.
- ²⁰ FALCONER, H. 1868. *Palaeontological Memoirs and Notes*, 2 : 601-625. Ed. C. Murchison, London.
- ²¹ FALCONER, H. 1868 : 619.
- ²² Evans had been unable to attend the conference, but he revisited Abbeville at the end of May to see the evidence again. In his letter to the *Athenaeum* of June 1863 (p. 747) he said that of more than 150 flint implements in his own collection from the Somme gravels there was not one that did not present characteristics of antiquity ; whereas the "suspected haches have not one of these characteristics", and when washed "their surface is as fresh as if made the same day. . . . Genuine implements", he continued, "have been hitherto comparatively rare at Moulin-Quignon. The suspected implements are now found in abundance".
- Falconer has recorded (1868 : 612-613) that fabrication of counterfeit implements was actively being carried on at Abbeville and Amiens, to meet the lively demand among collectors of antiquities caused by the authentic discoveries made by Boucher de Perthes. Strangers were usually asked to pay 5 francs for the privilege of detaching from its gravel bed the *hache* professing to have been discovered in situ by the *terrasier*.
- ²³ Keeping reported that on one occasion a workman pointed to an implement that he had just revealed. Keeping told him to stop digging so that he could remove it himself. "If the man had gone on digging the specimen out . . . I should most certainly have believed the specimen to have been a just one, as the gravel had not the appearance of having been recently removed ; but as soon as I commenced working I could tell directly that the gravel, for nearly the space of a foot round, had been moved, and I found the specimen near about in the centre of the new-made deposit". (H. Keeping in Evans, J. *Athenaeum*, July 4, 1863 : 19.)
- ²⁴ FALCONER, H. 1868. *Palaeontological Memoirs and Notes*, 2 : 604. Ed. C. Murchison, London.
- ²⁵ PRÜNER-BEY, F. 1866. *Sur la mâchoire humaine de La Naulette*. *Bull. Soc. Anthropol. Paris* (2) 1 : 584-592, 601-603.
- ²⁶ HUXLEY, T. H. 1863. *Evidence as to Man's Place in Nature* : 159. London.

IV. MIOCENE APES AND SPURIOUS "PLIOCENE MEN"

By the middle of the last century, largely through the active researches of the brilliant French lawyer turned palaeontologist, Edouard Lartet, some fossil "pithecoïds" were in fact already known in Europe, but there was little disposition among the scientists of that time to see in these forms the possible progenitors of man. In 1837 Lartet¹ discovered in the Miocene deposits at Sansan (Gers) remains of an extinct ape-like form which appeared to be ancestral to the modern gibbons.

He named it *Pliopithecus*, from the Greek πλειον more and πιθηκος ape. In 1856 he obtained from similar calcareous sands of Miocene age at Saint Gaudens part of the lower jaw of a more advanced type of ape, which he named *Dryopithecus*,² and declared it to be closely akin to man. But remaining predominant was the idea that *Man*, recognizable as such, may have already existed in the Miocene period. Writing earlier of the finds at Sansan, Lartet expressed it thus :

" Here are represented various degrees in the scale of animal life, up to and including the Ape. A higher type, that of the human kind, has not been found here ; but we must not hastily conclude . . . that it did not exist ".³

In view of this climate of opinion, it is not surprising that serious consideration was continually being given to human skulls and skeletons of entirely modern type unearthed from deposits of Pliocene or even earlier age in various parts of the world.

In 1860 the Italian geologist Ragazzoni discovered some human skull fragments in a shelly marine clay of Pliocene age at Castenedolo in Liguria.⁴ He could detect no indications that the overlying layers had been disturbed by the digging of a grave. Twenty years later, further remains were found in the same stratum : skeletons of a man, a woman and two children. Some of the bones were at a depth of over six feet below the present surface, and again the overlying layers appeared to be intact. The anatomist Professor G. Sergi who reported on these bones⁵ was convinced that they constituted proof that *Homo sapiens* already existed in Pliocene times. To explain their occurrence in a marine stratum he had to assume the " shipwreck " of a Pliocene family. The skulls could easily be matched in a modern European population. Although the bones have not been tested by modern methods of relative dating, and although taken seriously by more than one anatomist in recent years, their conditions of preservation stamp them as unquestionably post-Pliocene burials. The skeleton of the woman was in a contracted posture. Moreover, Professor Issel's examination revealed the fact that all the various fossils in the stratum were impregnated by salt, with the sole exception of the human bones.⁶

English deposits too have yielded skeletal remains claimed at various times as evidence of the great antiquity of our species. In 1855, a human jawbone was found during the digging of coprolites⁷ from the Red Crag sands at Foxhall, about four miles east of Ipswich. Heavily impregnated by iron oxides, the jaw matched the colour of the deposit in which it had lain, and was regarded by Dr. Robert Collyer, an American physician who described it in 1867,⁸ as probably contemporaneous. At the time great interest was taken in the Foxhall jaw. It was the English equivalent of the Moulin-Quignon jaw. Strangely enough the two are almost identical morphologically⁹ (Text-fig. 19). The Foxhall specimen shows on one side the rather rare feature of triple mental foramina¹⁰ but could probably be matched in any sufficiently large series of modern human mandibles, although commoner in early populations than in later. Falconer,¹¹ commenting on the use of mineral criteria in assessing the antiquity of fossil bones, said that the Foxhall jaw " although retaining a portion of its gelatine, is infiltrated through and through with iron. The section of the cortical layer is dark, oxide of iron is seen filling the

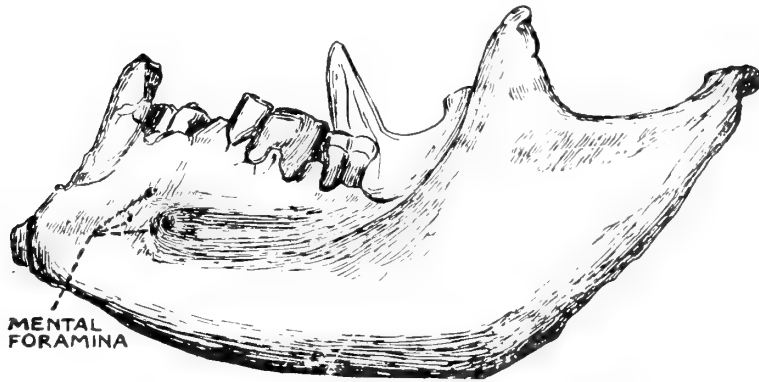


FIG. 19. The Foxhall jaw. *After Eiseley.* Nat. size. Whereabouts unknown.

Haversian canals ; a dark crust of the same material covers the walls of the cancelli ; coarse grains of sand, with red oxide of iron, line the walls of the dental canal ; and a vertical section of one of the fangs of a molar shows that the dentine is partly infiltrated by iron. The precise age of the jaw", he said, "is unknown, but is conjectured not to exceed that of the Roman occupation of England".

Interest in the Foxhall jaw was revived when Reid Moir advanced his claims to have found humanly chipped flints at the same level in the Foxhall sand-pit as the seam of nodules from which the "coprolite jaw" is alleged to have been extracted.¹² Collyer recorded that analysis of the jawbone showed that it contained 8 per cent. organic matter. Moir regarded this as consistent with the view that it was contemporaneous with the coprolite bed. He pointed out that fossil bones from the *basal* bed of the Red Crag are highly mineralized, with negligible organic content, but that those from the 16-ft. level in the Foxhall pit are commonly much less mineralized. He quoted analyses of five fossil bones from this level showing organic content ranging from 5.55 to 6.5 per cent. which he regarded as permitting him to regard the Foxhall jaw with 8 per cent. organic matter as possibly of Red Crag age.

We have already seen that the organic content of fossil bones is, considered by itself, very unreliable as a means of relative dating. It is unfortunate that the whereabouts of the Foxhall jaw is now unknown, in spite of energetic efforts to trace it in 1920,¹³ for there is little doubt that by means of modern methods of relative dating its degree of antiquity could be established with some certainty. There are few students of the subject today who take seriously the possibility that this specimen is older than Neolithic.

The most ridiculous Pliocene pretender was the Calaveras Skull, on which Bret Harte wrote a poem :¹⁴

*Speak, thou awful vestige of the earth's creation,
Solitary fragment of remains organic !
Tell the wondrous secret of thy past existence—
Speak thou oldest primate !*

*Which my name is Bowers and my crust was busted
Falling down a shaft in Calaveras County,
But I'd take it kindly if you'd send the pieces
Home to old Missouri.*

In 1866 a miner named Mattison was working at a depth of about 130 feet in his gold mine at Table Mountain in Calaveras county, California, when he encountered in the seam of auriferous gravel a very odd-shaped lump covered with a crust of lime. He took it home as a curiosity and eventually the specimen fell into the hands of J. D. Whitney, State Geologist of California, who chiselled away the crust and revealed the greater part of a human cranium, with adhering matrix containing bits of charcoal and a shell bead. He took the skull to Harvard College where it was examined and described.¹⁵ The skull had prominent cheek bones and was altogether quite typical of an American Indian (Text-fig. 20). Yet the gold-bearing stratum from which, allegedly, it came was of early Pliocene age, say more than 10 million years old. As Sir Arthur Keith once remarked, this made as much sense

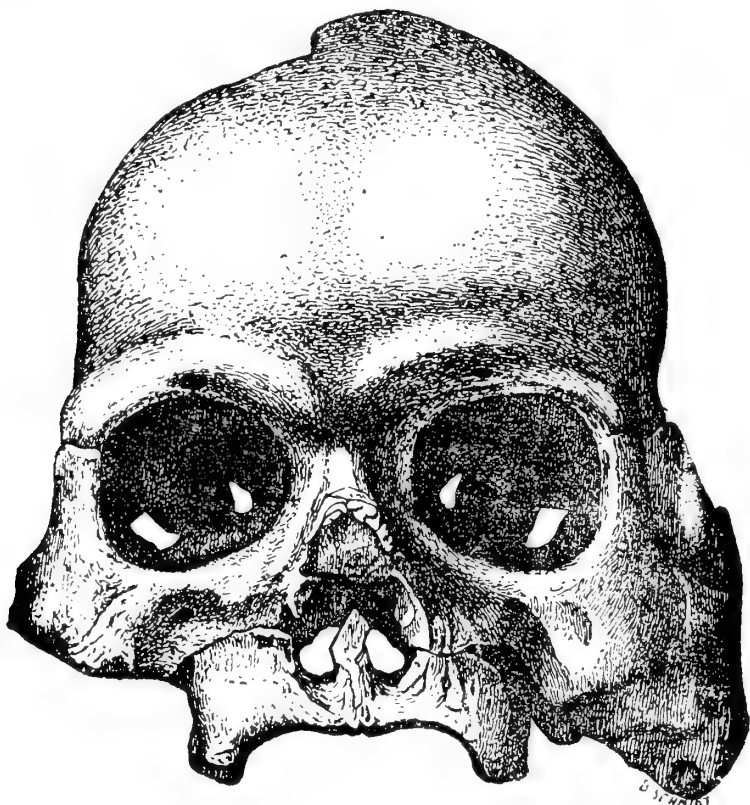


FIG. 20. The Calaveras skull. After T. Wilson. $\times \frac{2}{3}$ nat. size. Peabody Museum, Harvard University. Cat. No. 74963.

as finding an aeroplane in a church crypt that had been bricked up since Elizabethan times. But it seems that nobody dared laugh, and the evidence relating to the "Auriferous Gravel Man" was thoroughly examined and severely criticized by W. H. Holmes,²⁶ while Aleš Hrdlička, searching the collection in the U.S. National Museum, found two comparatively recent skulls preserved in precisely the same way, with incrustation of stalagmite, which had been collected from old caves in Calaveras county in 1857.¹⁷

It is very probable that the whole affair started as a cowboy hoax, and that Mattison was the dupe.¹⁸ It seems inconceivable now that it was ever taken seriously, but there was a strong subconscious desire to establish the antiquity of man in the New World, particularly in California where more than forty claims to have discovered early man have been advanced.¹⁹ Even as late as 1900 the level-headed Thomas Wilson of the U.S. National Museum read a paper at the International Congress of Anthropology and Prehistoric Archaeology in Paris strongly defending the antiquity of the Calaveras skull, citing as supporting evidence the alleged finding of flint arrowheads and stone mortars (*metates*) in the auriferous gravels of the same region. To bring the matter quite up to date it should be mentioned that the Evolution Protest Movement in Britain complained in 1951²¹ that the British Museum had suppressed important evidence by omitting all reference to the Calaveras skull from their handbook *The History of the Primates*, written by Sir Wilfrid Le Gros Clark.

It might be thought that the story of the Calaveras skull, entertaining though it is, would be scarcely worth mentioning in a survey of researches concerned with *dating* human remains. Curiously enough, however, as Sonia Cole has pointed out,²² it has an unsuspected importance in that very connection. Wilson quoted in support of his thesis the results of chemical analyses of the skull and of a bone of an extinct rhinoceros from the auriferous gravel. The analyses,²³ rearranged below, showed

Calaveras skull		Bone of Rhinoceros hesperius	
%		%	
Calcium phosphate . .	39·79	Calcium phosphate . .	49·40
Calcium carbonate . .	62·03	Calcium carbonate . .	18·33
Magnesium carbonate .	1·86	Calcium fluoride . .	4·77
Silica	1·44	Silica	22·70
Iron oxide	0·81	Iron oxide	4·58
Water and organic matter	Traces	Magnesia	Traces
	99·93		99·78

that the skull and the extinct rhinoceros bone had both lost almost all their organic matter ("gelatine" of earlier writers), and that a large proportion of the bone of the skull had been replaced by calcium carbonate. Wilson argued on this basis that the Calaveras skull was "fossilized". In fact the percentages of the various minerals composing the two bones are very different. Moreover, as Holmes pointed out, under certain conditions bones can lose their organic matter in a few centuries; while if buried in limestone caves, where percolating waters are continually dissolving

and redepositing calcareous matter, they may be replaced by calcium carbonate in a comparatively short time.

Vayson de Pradenne in his book on frauds published in 1932²⁴ drew attention to a feature of the Calaveras analyses which had previously been overlooked and which completely condemns Wilson's thesis. Vayson was apparently the first person in the present century to recognize the significance of Adolphe Carnot's discovery in the eighteen-nineties that the accumulation of *fluorine* in fossil bones provides a valuable means of relative dating. Looking again at the analyses of the Calaveras specimens we see that the genuinely fossil rhinoceros bone contains nearly 5 per cent. calcium fluoride, whereas the human skull contains none—"or no doubt traces which escaped the chemist", to quote the cautious words of Vayson, who concluded: "There is thus no possible comparison between the ages of the two bones. One is geologically ancient, the other modern".

SECTION IV (Notes)

- ¹ LARTET, E. 1837. Note sur la découverte recente d'une mâchoire de singe fossile. *C. R. Acad. Sci.*, Paris, **4** : 91-92 ; 583-584.
- ² LARTET, E. 1856. Note sur un grand Singe fossile qui se rattache au groupe des Singes supérieurs. *C. R. Acad. Sci.*, Paris, **43** : 219-223.
The name *Dryopithecus*, derived from the Greek words δρυς oak tree and πιθηκος ape, was used because fossil oak leaves were found in the Miocene deposits containing remains of this ape.
- ³ BOULE, M. & VALLOIS, H. V. 1957. *Fossil Men* : 17, 18. London. Also see Fischer, P. 1872. Note sur les travaux scientifiques d'Edouard Lartet. *Bull. Soc. géol. Fr.*, Paris (2) **29** : 252.
- ⁴ RAGAZZONI, G. 1880. La collina di Castenedolo. *Commentari dell'Ateneo di Brescia* : 120. Brescia.
- ⁵ SERGI, G. 1884. L'Uomo Terziario in Lombardia. *Arch. Antrop. Etnol.*, Firenze, **14** : 303-318, pl. 1.
- ⁶ ISSEL, A. 1889. Cenni sulla giacitura dello scheletro umano recentemente scoperto nel Pliocene de Castenedolo. *Boll. Paletol. ital.*, Parma, **15** : 89.
- ⁷ Coprolites, *sensu stricto*, are fossilized excreta, but this name (derived from κοπρος dung) has been applied also to brown or black phosphatic nodules of similar appearance, but of inorganic origin, formed on the sea-floor. Such are the "coprolites" in the Red Crag of Suffolk. The Crag "coprolites" with associated fossil bones and teeth were extracted commercially during the last century from 1847 onwards. Ground down and treated with sulphuric acid these materials became superphosphate fertiliser for the land. See Oakley, K. P. 1944. Man and the Migrations of Phosphorus. *Trans. S.E. Union Sci. Soc.*, London, **49** : 29, 30.
- ⁸ COLLYER, R. H. 1867. The Fossil Human Jaw from Suffolk. *Anthrop. Rev.*, London, **5** : 221.
- ⁹ KEITH, A. 1925. *The Antiquity of Man*, **1** : 273. London.
- ¹⁰ EISELEY, L. C. 1943. A Neglected Anatomical Feature of the Foxhall Jaw. *Trans. Kans. Acad. Sci.*, Topeka, **48** : 57-59.
- ¹¹ FALCONER, H. 1868. *Palaeontological Memoirs and Notes*, **2** : 616. Ed. C. Murchison. London.
- ¹² REID MOIR, J. 1921. Further Discoveries of Humanly-fashioned Flints in and beneath the Red Crag of Suffolk. *Proc. Prehist. Soc. E. Angl.*, London, **3** : 390-411.
- ¹³ REID MOIR, J. 1921 : 397.
- ¹⁴ BRET HARTE. 1887. To the Pliocene Skull. *Complete Poetical Works* : 256-257. London.

- ¹⁵ WHITNEY, J. D. 1879. The Auriferous Gravels of the Sierra Nevada of California. *Mem. Harv. Mus. Comp. Anat.*, Cambridge, Mass., **6** : 258-288.
- ¹⁶ HOLMES, W. H. 1899. A Review of the evidence relating to the Auriferous Gravel Man in California. *Rep. Smithsonian. Instn.*, Washington, **1899** : 419-472.
- ¹⁷ HRDLÍČKA, A. 1907. Skeletal Remains suggesting or attributed to Early Man. *Smithson. Inst. Bur. Ethn.*, Washington, **33** : 21-28.
- ¹⁸ COLE, S. 1955. *Counterfeit* : 133. London.
- ¹⁹ HEIZER, R. F. 1950. Observations on Early Man in California. *Rep. Arch. Surv. Univ. Calif.*, Los Angeles, **7** : 5-9.
- ²⁰ WILSON, T. 1902. La haute ancienneté de l'homme dans l'amérique du Nord. *C. R. Congr. Int. Anthropol. Arch. Préhist.*, Paris (XIIe sess., 1900) : 158-170.
- ²¹ FILMER, W. E. 1951. How They Choose Our Ancestors, A Protest to the Trustees of the British Museum. *Evolution Protest Movement*. 11 pp. London.
- ²² COLE, S. 1955. *Counterfeit* : 134. London.
- ²³ Analyses by Sharples, and originally published by Whitney (1879 : 244, 269—see Note 15).
- ²⁴ VAYSON DE PRADENNE, A. 1932. *Les Fraudes en Archéologie Préhistorique* : 142, footnote. Paris.

V. CRO-MAGNON AND OTHER FOSSIL MEN : THE PALAEOOLITHIC SEQUENCE

Looking back over the history of human palaeontology, it is strange to find that when genuine fossil men were discovered, doubts about them were sometimes as persistent as the mistaken beliefs in spurious specimens. The recurring prejudice against the Pleistocene men of Cro-Magnon is a case in point.

In 1868, when the railway from Périgueux to Agen was being constructed through Les Eyzies in the Vézère valley (Dordogne), clearance of material from the hillside revealed an *abri* or rock-shelter containing layers of occupation debris, crammed with bones and teeth of reindeer and other animals of the glacial fauna, together with Palaeolithic artifacts in flint and bone. Full excavation of this site, known as Cro-Magnon,¹ was undertaken by the geologist Louis Lartet,² son of the eminent Edouard. At the back of the *abri*, below a ledge of rock and completely sealed in by ancient rock-falls (Text-fig. 21), he found a layer containing remains of five human skeletons referable to our own species *Homo sapiens*. These had evidently been buried ceremonially, for they were accompanied by red ochre and by strings or necklaces of sea shells (*Littorina*). Although the skeletons were at the top of the deposits with Palaeolithic implements and food refuse, the layer which contained them "included an unbroken series of hearths which actually touched the overhanging rock except for a short space at the very back".³ There was no doubt in the mind of the excavator that the skeletons had been interred during Pleistocene times. Yet, Boyd Dawkins,⁴ one of the leading authorities in Britain at that time on cave deposits, wrote in 1880 that the remains of Cro-Magnon Man were in a deposit *overlying* the ancient refuse heaps, and were "therefore later than the Palaeolithic". While in 1895, the eminent French prehistorian Gabriel de Mortillet, to whom we owe the basic classification of Old Stone Age cultures, stated categorically in regard to the Cro-Magnon skeletons : "il est facile de montrer qu'elles sont récentes".⁵ To his mind one of the indications that they were Recent was the fact that the skull of the "Old Man" (Plate 2) protruded from the deposits into

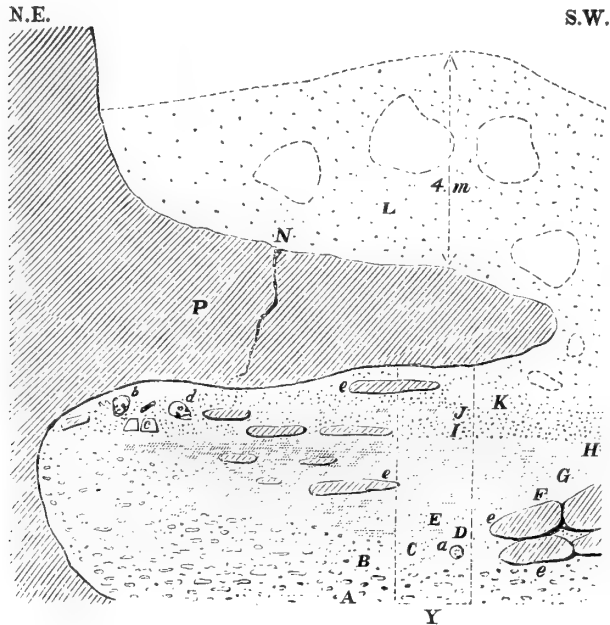


FIG. 21. Section through the Cro-Magnon rock-shelter. *After L. Lartet (in E. Lartet & Christy).* A, C, E, K, debris of the soft limestone; B, D, F, layers of ashes (hearths); G, red earth with bones; H, thickest layer of ashes, with animal bones and flints; I, yellowish earth with bones and flints; J, thin bed of hearth material; P, projecting roof of hard limestone; a, elephant tusk; b, bones of "Old Man" [Cro-Magnon I]; c, block of gneiss; d, human bones; e, roof falls.

the vacant space, and judging from a patch of stalagmitic incrustation, and from the corroded state of the facial bones, it had never been completely covered by Palaeolithic debris. To reassure the reader that this is not necessarily a valid reason for doubting the antiquity of bones, it is worth recalling that a *Neanderthal* skull was found in a precisely similar uncovered state on the floor of one of the caves in Monte Circeo. As a further supposed indication that the Cro-Magnon burials were Recent, de Mortillet pointed out that the associated *Littorina* shells had retained their "epidermal" colour. However, it is now well known that shell-pigments are sometimes remarkably persistent. The fossil shells of *Theodoxus* in the Lower Palaeolithic gravels at Swanscombe, for instance, have retained their colour pattern.

It was agreed by all that the skeletons in question were Stone Age *burials*: the differences of opinion related simply to the date of interment. It may be that de Mortillet was prejudiced against accepting them as Palaeolithic simply because he had for long been firmly convinced that no ceremonial burials were older than Neolithic.⁶

Even as recently as 1924 Grant MacCurdy allowed a hint of scepticism about their dating to creep into his account of the Cro-Magnon skeletons, saying⁷ "The . . . remains look as fresh as if they had been found in cave deposits of Neolithic age"

and furthermore "In some respects . . . do resemble the early Neolithic races more closely than do certain Aurignacian [i.e. late Palaeolithic] skeletons of which the age is beyond question". At the present day, the Cro-Magnon remains are unreservedly accepted as Palaeolithic by those best qualified to judge the evidence,⁸ but if doubts ever recurred radiocarbon dating should provide an objective indication of their actual age (see p. 150).

Appreciation of the significance of the fossil human remains that eventually passed muster depended to a considerable extent on the building up of a framework of relative chronology into which the various finds could be fitted. Especially important in this connection were the researches of Edouard Lartet in the caves of the Dordogne in south-western France, where he was assisted by the banker Henry Christy in 1863 and 1864. Their excavations in the caves or rock-shelters of Laugerie Haute, Les Eyzies, Le Moustier and La Madeleine showed that the "Age of simply worked stone", or as we would now say Palaeolithic period, was not a single phase of human culture, but a succession of phases, which were locally datable by the associated fossil animal remains, on the principle that the composition of the fauna changed in course of time. On the basis of the finds in the Dordogne caves, Lartet had proposed in 1860 to distinguish the following periods:⁹

- (4) Period of Aurochs (*Bos primigenius*), early Post-Pleistocene in modern terms
- (3) Reindeer Period, = Late Pleistocene in modern terms
- (2) Period of Mammoth (*Elephas primigenius*) and Woolly Rhinoceros, '*Rhinoceros tichorhinus*' [= *Coelodonta antiquitatis*]
- (1) Cave-bear Period.

Later he recognized that the Cave-bear and Mammoth periods were scarcely separable; while another palaeontologist, Garrigou,¹⁰ pointed out that these periods, when glacial or cold-tolerant animals predominated, were preceded by times when the fauna had a warm aspect, and included such forms as *Hippopotamus*, *Elephas* (*Palaeoloxodon*) *antiquus* and Merck's rhinoceros (*Dicerorhinus kirkbergensis*). In the eighteen-seventies James Geikie and others realized that the river-drifts with this warm fauna and Palaeolithic hand-axes, as at Abbeville and St. Acheul in the Somme valley, represented one or more *interglacial* periods.

Some students of the Palaeolithic in Lartet's day disagreed with his use of faunal subdivisions of prehistoric times. They pointed out that the incidence of the various animal species would have varied from region to region, and that the differences between the contents of one Palaeolithic occupation deposit and another might simply reflect the preferences of different groups of hunters. These criticisms had elements of truth in them, but the discovery of the same broad faunal succession at site after site eventually proved that, within certain limits, fossils provide a good basis for subdivision of the Pleistocene period.

Archaeologists such as Gabriel de Mortillet considered that it was better to subdivide the Palaeolithic period into stages based on the various types of artifact which successively prevailed in Western Europe. In 1867, de Mortillet¹¹ developed

a scheme of relative chronology based on the sequence of Palaeolithic industries found in France. The stages or "epochs" were named after the sites where the industries were typically represented, as follows :—

Époque de la Madeleine (= Reindeer Age)

Époque de Solutré

Époque d'Aurignac

Époque du Moustier (= early part of Cave-bear-Mammoth Age)

Époque de Chelles (= period of *Elephas antiquus*).

De Mortillet was uncertain where the Aurignacian epoch should be placed. At first (in 1867) he followed Lartet's suggestion and placed it late in the Cave-bear-Mammoth Age ; next (in 1868) he placed it *after* Solutré, and then finally (in 1872), dropped it out of his scheme altogether.

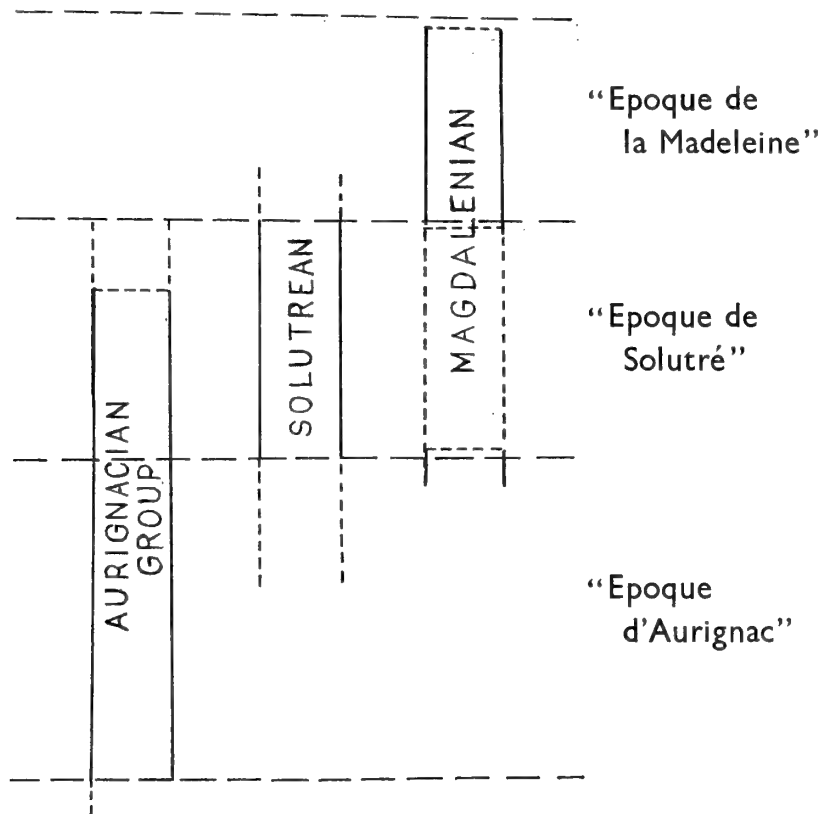


FIG. 22. Time relationships of the main Upper Palaeolithic culture-groups.

When the names Chellean, Mousterian, Aurignacian and so on were introduced, they were unquestionably intended as the names of *periods*,¹² but during the present century they have acquired a different significance, and have been mainly used as the names of *cultures*.

This change occurred through evidence accumulating, as research extended over wider areas, which showed that the Palaeolithic industries named in de Mortillet's scheme did not follow one another in a simple linear series, but were manifestations of separate cultural traditions which were in part contemporaneous (Text-fig. 22). Thus, although the Aurignacian culture began before the Solutrean, Late Aurignacian industries are geologically younger than Early Solutrean. Hamy,¹³ writing in 1870, was the first to recognize that Solutrean and Magdalenian cultures were largely contemporaneous.

In spite of these complications, the following classification, of the broad cultural subdivisions of the Palaeolithic in Western Europe, was generally agreed within the first decade of the present century :

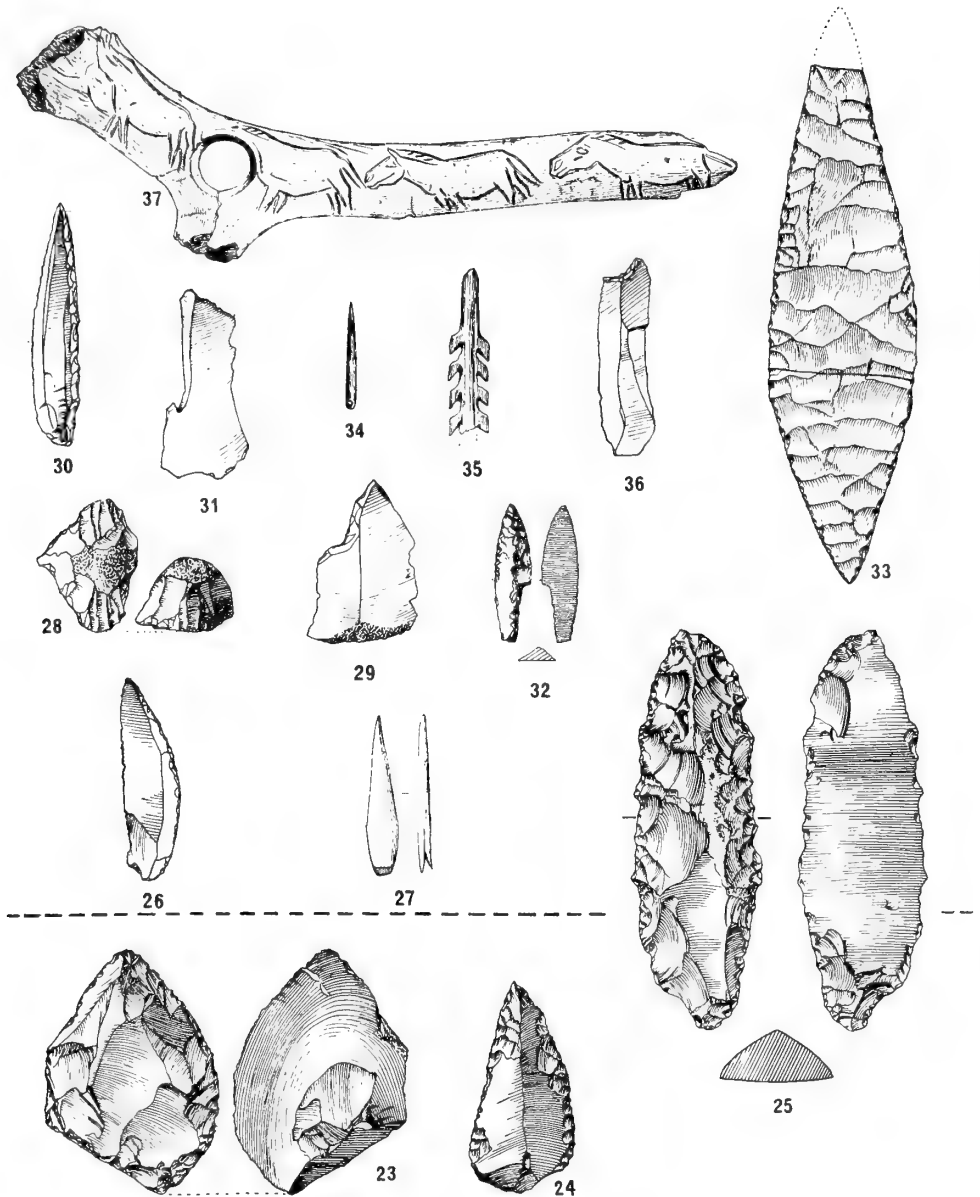
Magdalenian	}	Upper Palaeolithic
Solutrean		
Aurignacian		
Mousterian	—	Middle Palaeolithic
Acheulian	}	Lower Palaeolithic.
Chellean		

The Lower Palaeolithic, or River Drift period, when men lived mainly in the open, is represented almost entirely by implements chipped in stone. The artifacts usually regarded as most characteristic of this period are "core-tools",¹⁴ that is to say made by striking flakes from a nodule or pebble so that the residual core forms the implement. Such are the typical Chellean and Acheulian hand-axes (Text-figs. 4, 8-10), called *haches* or *coups de poing* by the earlier French archaeologists.

In the succeeding Middle Palaeolithic period, men sometimes lived in the open, but when the climate became severe they took to making their homes in shallow caves or rock-shelters. The Middle Palaeolithic stage, represented by the Mousterian industries, was distinguished by the frequency with which tools were chipped out of *flakes* (Text-figs. 23, 24). Although bones were occasionally used (for example as anvils), no attempt was made in this stage to work them into implements or to decorate them.

In Upper Palaeolithic cultures, flint tools were mostly made on parallel-sided flakes, or *blades* (Text-figs. 26, 30, 36), while bone, antler and ivory were extensively worked (Text-figs. 6, 27, 34, 35, 37). Many groups of hunters of this period occupied caves, or rock-shelters. They were responsible for the well-known cave-art of southern France and Spain. Other groups, wherever conditions were suitable, lived in huts or tents in the open. The type-station of Solutrean culture (Text-fig. 33), near Macon in south-east France, is an example of one of these open sites. Some of the mammoth and reindeer hunters living on open sites in Eastern Europe carved and engraved ivory and other bony materials with remarkable artistry.

Particularly important from the point of view of using artifacts for relative dating is the question of the chronological relationship of the Palaeolithic cultures to the faunal and climatic stages of the Pleistocene, in other words the dating of the Early Stone Age or Palaeolithic cultures in terms of glacial and interglacial periods. James



FIGS. 23-37. Representative Middle and Upper Palaeolithic artifacts, arranged stratigraphically. Those below the broken line are Middle Palaeolithic, those above Upper Palaeolithic. "Proto-Solutrean" is in Middle Upper transition. \times circa $\frac{2}{3}$ nat. size.

FIG. 23. Mousterian side-scraper on a flake of flint. Le Moustier rock-shelter, near Peyzac (Dordogne). B.M. (N.H.) E.322a.

FIG. 24. Mousterian point on flake (flint). Le Moustier rock-shelter. B.M. No. E.324.

- FIG. 25. "Proto-Solutrean" (cf. Szeletian) flint point. Nietoperowa Cave, Jerzmanowice, Ojcow district, Poland. B.M. (N.H.) E.202.
- FIG. 26. "Lower Aurignacian" (Châtelperronian=Earlier Perigordian) flint knife-point. Châtelperron. B.M. (N.H.) E.1217.
- FIG. 27. "Lower Aurignacian" (Châtelperronian) split-base bone point. Sergeac (Dordogne). *After Peyrony*.
- FIG. 28. "Middle Aurignacian" (Aurignacian s.s.) flint end-scraper. Cae Gwyn, Vale of Clwyd, N. Wales. B.M. (N.H.) E.1318.
- FIG. 29. "Middle Aurignacian" (Aurignacian s.s.) flint *burin busqué*. Cro-Magnon (Dordogne). B.M. (N.H.) E.1306.
- FIG. 30. "Upper Aurignacian" (Gravettian=Later Perigordian) flint knife-point. Laussel (Dordogne). B.M. (N.H.) E.1218.
- FIG. 31. "Upper Aurignacian" (Gravettian) flint graver or burin. Langerie Haute (Dordogne). B.M. (N.H.) E.1320.
- FIG. 32. Solutrean shouldered "willow-leaf" flint point, showing pressure-flaking. Bourdeilles (Dordogne). B.M. (N.H.) E.1331.
- FIG. 33. Solutrean "laurel leaf" bifacial flint blade. Solutr , France. *After de Mortillet*.
- FIG. 34. Magdalenian polished bone needle. Bruniquel Caves (Tarn-et-Garonne). B.M. (N.H.) 39306.
- FIG. 35. Magdalenian-type biserially barbed point in antler. Kent's Cavern, Torquay. B.M. (N.H.) E.70.
- FIG. 36. Magdalenian concave flint end-scraper. Limeuil (Dordogne). B.M. (N.H.) E.1321.
- FIG. 37. Magdalenian antler tool; perforated and decorated with incised horses. La Madeleine rock-shelter (Dordogne). *After de Mortillet*.

Geikie began to deal with this question to some extent in his work on the Great Ice Age. In the second edition (1877) he noted the possibility that human origins were preglacial, but in the next edition (1894), in spite of the current clamours of believers in eoliths, he stated¹⁵ that there was still no acceptable evidence that man was an inhabitant of Europe either before or during the First Interglacial period, when the characteristic elephant was *Elephas (Archidiskodon) meridionalis*. He pointed out that in contrast there were abundant traces of man in the form of Chellean and Acheulian hand-axes associated with remains of *Elephas (Palaeoloxodon) antiquus*, dating from the succeeding interglacial.

There was for a long time much confusion—there still is some—between deposits of the Second and the Third interglacial periods, partly due to the fact that *Elephas (Palaeoloxodon) antiquus*, mainly characteristic of the Second, persisted in some areas into the Third Interglacial. Perhaps through this confusion, Geikie fell into the error of mistaking certain events of the Fourth Glaciation for events of the "Third". Thus in 1894¹⁶ he attributed the main occupation of the French caves to the time of the "Third", whereas in fact they had been mainly occupied, as he later recognized, during the Fourth or last main glaciation. On the other hand he had already correctly inferred¹⁷ that the later Palaeolithic men were hunting mammoth (*Elephas (Mammuthus) primigenius*) and reindeer during the time of formation of the Younger Loess, a deposit of wind-borne dust which blanketed extensive areas of Europe and Asia under the steppe conditions that prevailed during certain phases of the Last Glaciation.

For a number of years there was considerable uncertainty about the correlation of the Mousterian stage of culture with the glacial-interglacial sequence. W. H. L. Duckworth said in 1912:¹⁸ "In attempting to adjust the scale of glacial periods to that provided by the succession of implements, it is suggested that a commencement should be made by considering the period designated Mousterian. If the position of the Mousterian period can be correlated with a definite subdivision of the Ice Age, the other periods will fall into line mechanically".

The geologists Penck & Brückner found evidence early in this century¹⁹ that there had been four distinct extensions of ice over the foreland of the Alps, and these they named after the Bavarian valleys where the respective moraines and outwash gravels were well developed, in order of time: Günz, Mindel, Riss and Würm. These were presumed to be the First, Second, Third and Fourth Glaciations already recognized by Geikie.²⁰

Emil Bächler reported in 1906²¹ that the cave of Wildkirchli at 4,923 feet above sea-level in the Swiss Alps had been occupied by Mousterian Man at a time when the fauna of the area was of temperate type, although it did not include any definite time indicator such as *Elephas (Palaeoloxodon) antiquus*. As the entrance to the cave was above the snow-line of the Würm ice-age, Penck²² inferred that Mousterian Man had occupied it during the preceding, Riss-Würm interglacial period. At a number of other localities, for example at Spy in Belgium, and in many French caves, Mousterian industries had been found associated with an arctic or tundra fauna including mammoth (*Elephas (Mammuthus) primigenius*), woolly rhinoceros and reindeer. Penck and some other authorities²³ regarded the main or "cold" Mousterian as dating from the Third Glaciation; but as it directly underlay Aurignacian layers at many of the sites, there was really no doubt that it dated from the early stage of the Fourth, or Würm, glaciation.

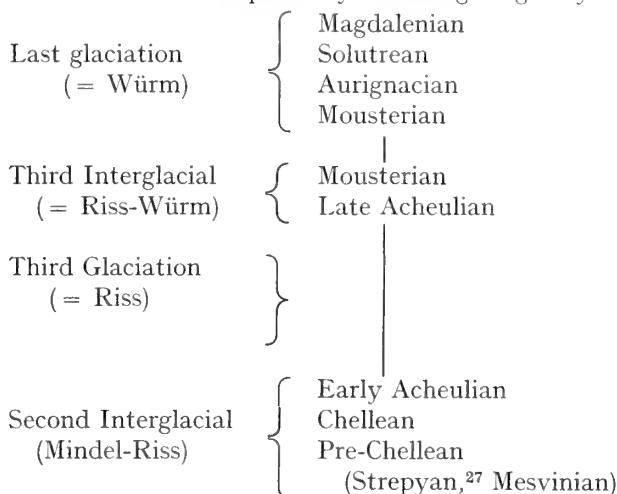
The term Mousterian was formerly used by archaeologists much more widely than at present, and covered flake industries which are now known as Clactonian and Levalloisian. Some of these Mousterian-like industries were being made during and before the Third Glaciation. However, even in the restricted sense, Mousterian culture certainly existed during Third Interglacial times. For example, at Taubach near Weimar, Mousterian artifacts had been discovered in 1895²⁴ associated with remains of *Elephas (Palaeoloxodon) antiquus*, also with two human teeth which gave rise to much discussion on account of certain ape-like traits. The Taubach teeth are now recognized as representing a variant of the Neanderthal type.

There is no longer any doubt that the "cold" or main Mousterian industries date from the first part of the Fourth Glaciation, and that some "warm" Mousterian belonged to Third Interglacial times. However, the possibility that some of the "warm" Mousterian in Southern Europe (for example at Krapina in Yugoslavia) were really contemporaneous with an early interstadial of the Fourth Glaciation still has to be considered.

In 1873,²⁵ Merck discovered in the cave of Kesslerloch, in Switzerland, numerous Palaeolithic artifacts, including engraved reindeer antlers, which were later identified

as Magdalenian. Penck²⁶ showed that this occupation of the cave occurred during the retreat of the ice in the final stage of the Last Glaciation.

By the end of the first decade of this century, although there were many and varying interpretations of the evidence, it was beginning to be recognized that the cultures of Palaeolithic Man were probably datable geologically as follows :—



Although the increase of our knowledge of the Palaeolithic in the last fifty years, particularly through the extension of research beyond Europe, has greatly complicated the picture, the sequence of culture stages established in France in the last century provided a useful provisional scheme of relative chronology for almost all the fossil men then known. The following archaeologically dated remains, among others, had been reported before World War I :

- Magdalenian : La Madeleine (1864) ; Bruniquel (1863-64) ; Laugerie Basse (1872) ; Chancelade (1888). *Homo sapiens*.
 Solutrean : Le Placard (1882) ; Pair-non-Pair (1888). *Homo sapiens*.
 Aurignacian : Engis II (1830) ; Cro-Magnon (1868) ; Brunn II (1891) ; Predmost (1894) ; Grimaldi (1902-06) ; Combe Capelle (1909). *Homo sapiens*.
 Mousterian : Sipka (1880) ; Spy (1886) ; Taubach (1887, 1892) ; Krapina (1899) ; Le Moustier (1908) ; Ehringsdorf (1908) ; La Chapelle-aux-Saints (1908) ; La Ferrassie (1909). *Homo neanderthalensis*.

Thus, in the early part of this century it seemed clear enough that, if one excluded remains of doubtful age such as the skeleton found with Acheulian hand-axes at Galley Hill in 1888,²⁸ the earliest relics of our own species, *Homo sapiens*, were Upper Palaeolithic. It seemed equally clear that *Homo neanderthalensis* was Middle Palaeolithic. The question of the nature of the precursors of these two species presented a great problem, and the evidence bearing on it fifty years ago was puzzling and of very unequal value.

SECTION V (Notes)

- ¹ In *patois*, *cro magnon* means great hole. The rock-shelter is now occupied by part of the hotel named after it.
- ² LARTET, L. 1868. A Burial Place of the Cave-dwellers of Perigord, in Lartet, E. & Christy, H. *Reliquae Aquitanicae*, **6** : 62-72. Ed. T. R. Jones. London.
- ³ MACCURDY, C. G. 1924. *Human Origins*, **1** : 381. New York.
- ⁴ DAWKINS, W. B. 1880. *Early Man in Britain* : 206-207. London.
- ⁵ MORTILLET, G. & A. DE. 1900. *Le Préhistorique* : 312. 3rd ed. Paris.
- ⁶ SOLLAS, W. J. 1924. *Ancient Hunters* : 446. 2nd ed. London.
- ⁷ MACCURDY, C. G. 1924. *Human Origins*, **1** : 382-383. New York. F. Pruner-Bey has left it on record that before treatment the human bones were tested for gelatine content, which proved to be the same as that of Palaeolithic reindeer bones at this site (Lartet & Christy. 1868. *Reliquae Aquitanicae*, **7** : 73).
- ⁸ VALLOIS, H. V. 1952. Catalogue des Hommes Fossiles. *C. R. Congr. Géol. Int.* (XIXe sess., Algiers) 1952 : 132. The archaeological horizon of the Cro-Magnon skeletons is stated to be "Aurignacien-niveau des pointes à base fendue". (For dating of Aurignacian remains see p. 150.)
- ⁹ LARTET, E. 1860, quoted in *Bull. Soc. Anthropol. Paris*, **6** (1865) : 334.
- ¹⁰ GARRIGOU, F., quoted by Daniel, G. E. 1950. *A Hundred Years of Archaeology* : 100. London.
- ¹¹ In *Matériaux de l'Histoire positive et naturelle de l'Homme*, **3** (1867) : 193-195. G. de Mortillet regarded the stage of culture represented at Laugerie Haute as *following* that represented at Aurignac, which he placed with the stage of Le Moustier in "première époque des cavernes". A year later (1868, **4** : 457) he proposed the name "Époque de Solutré" as the equivalent of "Époque de Laugerie Haute" but regarded it as coming *before* Époque d'Aurignac. In his later classification (1872 *C. R. Int. Anthropol. Arch. préhist.*, Bruxelles (VIe sess.) : 442-443) he eliminated the Aurignacian epoch altogether. Many authors at the end of the last century and beginning of the present followed de Mortillet in limiting the Palaeolithic stage-names to Chellean, Mousterian, Solutrean and Magdalenian.
- ¹² DANIEL, G. E. 1950. *A Hundred Years of Archaeology* : 106, 108-109. London.
- ¹³ HAMY, E. T. 1870. *Précis de Paléontologie Humaine* : 336-340. Paris.
- ¹⁴ It is evident from William Pengelly's address on the Antiquity of Man (*Rep. Brit. Ass.*, **1883** : 558) that he was the first archaeologist to classify Palaeolithic industries on the basis of distinction between core-tools and flake-tools. Thus, speaking of the stone artifacts from Kent's Cavern, he said : "While all . . . are Palaeolithic . . . a mere inspection shows that they belong to two distinct categories. Those found in the Breccia—that is to say the more ancient—were formed by chipping a flint nodule or pebble into a tool, while those of the Cave-earth—the less ancient series—were fashioned by first detaching a suitable flake from the nodule or pebble, and trimming the flake—not the nodule—into a tool".
- ¹⁵ GEIKIE, J. 1894. *The Great Ice Age* : 689. 3rd ed. London.
- ¹⁶ GEIKIE, J. 1894 : 690.
- ¹⁷ GEIKIE, J. 1894 : 689.
- ¹⁸ DUCKWORTH, W. H. L. 1912. *Prehistoric Man* : 118. Cambridge.
- ¹⁹ PENCK, A. & BRÜCKNER, E. 1900. *Die Alpen im Eiszeitalter*. 3 vols. Leipzig.
- ²⁰ In his Munro Lectures (Geikie, J. 1913. *On the Antiquity of Man in Europe*) he gave a revised version of a classification of glacials and interglacials which he had proposed in 1895 (*J. Geol.*, Chicago, **3** : 241) and correlated it with the scheme later put forward by Penck & Brückner, as follows :

Scanian or 1st Glacial	—	Günz
Norfolkian or 1st Interglacial	—	Günz-Mindel
Saxonian or 2nd Glacial	—	Mindel
Tyrolian or 2nd Interglacial	—	Mindel-Riss

Polonian or 3rd Glacial	—	Riss
Durnentian or 3rd Interglacial	—	Riss-Würm
Mecklenburgian or 4th Glacial	—	Würm
Lower Forestian or 4th " Interglacial "		"Post-Würmian"
Lower Turbarian or 5th " Glacial "		retreats
Upper Forestian or 5th " Interglacial "		and
Upper Turbarian or 6th " Glacial "		advances

Geikie's use of names for the interglacial stages had much to recommend it.

- 21 BÄCHLER, E. 1906-07. Die prähistorische Kulturstätte in der Wildkirchlieden-Alphöhle (Säntisgebirge, *Verh. schweiz. naturf. Ges.*, St. Gallen).
- 22 PENCK, A. & BRÜCKNER, E. 1909. *Die Alpen im Eiszeitalter*. 3 vols. Leipzig.
- 23 DUCKWORTH, W. H. L. 1912. *Prehistoric Man* : 120. Cambridge. For discussion.
- 24 NEHRING, A. 1895. Über Kinderzahn aus dem Diluvium von Taubach bei Weimar. *Z. Ethn.*, Berlin, **27** : 425-433. See also Keith, A. 1925. *Antiquity of Man*, **1** : 191. London.
- 25 MERCK, C. 1876. *Excavations at the Kesserloch near Thayngen, Switzerland* (translated from German by J. E. Lee). London.
- 26 PENCK, A. 1901. Die Glacialbildungen um Schaffhausen und ihre Beziehungen zu den praehistorischen Stationen des Schweizervbildes und von Thayingen. Reprinted from *N. Denkschr. schweiz. naturf. Ges.*, Zurich, **35** (1896).
- 27 The name Strepyan was applied by Rutot to simply-flaked nodule tools found in certain terrace gravels in Belgium, and regarded by him as prototypes of the Chellean industry, comparable with the Pre-Chellean recognized by V. Commont in the Somme Valley. From gravels of similar age at Mesvin, Rutot described flake-tools which foreshadowed the Mousterian, but which were "eolithic" in their crudity. The "Mesvinian" industry, subject of much controversy (Sollas, W. J. 1924. *Ancient Hunters* : 157), was eventually identified with the better defined flake-industry found in the *Elephas (Palaeoloxodon) antiquus* gravel at Clacton-on-Sea, Essex, and named Clactonian by Hazzledine Warren (*Trans. S.E. Union Sci. Soc.*, London, **1926** : 47, footnote). Much of the Pre-Chellean, and the Chellean industries, were eventually classed as phases of Acheulian culture.
- 28 The evidence for the antiquity of the Galley Hill skeleton was re-examined in 1948. The suggestion that it had been buried in the Swanscombe gravel in post-Pleistocene times was confirmed by comparison of its *fluorine* content with that of a series of fossil bones from local Pleistocene deposits (Oakley, K. P. & Montagu, M. F. A. 1949. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, **1** : 25-48). In 1960, after nitrogen analysis had established the percentage of residual collagen in this skeleton, portions of the humeri were found to be adequate for determining the radiocarbon age of this "historic" specimen (see p. 150) now preserved (with accurate casts of the expended portions) in the Anthropology Sub-Department of the British Museum (Natural History).

VI. DATING THE EARLIEST MEN : JAVA AND HEIDELBERG

The filling of the big blank between Middle Palaeolithic or Neanderthal Man on the one hand and the Tertiary apes on the other, began in the eighteen-nineties through the compulsive zeal of a young Dutch army doctor, Eugene Dubois, who had been inspired by the writings of Darwin and other evolutionists, and regarded the tropics as the area in which we may expect to find the fossilized precursors of man.¹ Posted to the Dutch East Indies as an army physician in 1887, he found an opportunity to excavate caves in Sumatra, and later was commissioned to make a reconnaissance of fossil-bearing deposits in Java. Collecting from ancient river gravels at Kedung Brubus in Central Java, he discovered on November 24th 1890 a fragment of a

fossilized human jawbone.² Unfortunately it was undiagnostic, lacking the chin region and the teeth, apart from the root of one of the canines, or eye-teeth ; but it was an encouraging find, for the same deposits yielded remains of animals now extinct in Java, such as the tapir.

Next year, continuing westwards up the valley of the Bengawan, or Great Solo River, Dubois reached some promising exposures of volcanic tuffs and sands near the river-side village of Trinil a few miles from the foot of the volcano Mt. Lawu. It was then August, late in the dry season when the river is at its lowest, and consequently Dubois was able to dig into a bone-bearing layer which was often inaccessible through flooding. His search was soon rewarded by discovering among the fossils brought out of the excavations by his workmen an upper molar tooth of ape-like form (Text-fig. 38, *right*) which he provisionally identified as *Anthropopithecus*³—the Latin name then in use for chimpanzee. Although chimpanzees are confined to Africa, this identification did not seem unreasonable at the time because a fossil jaw fragment of an ape⁴ similar to chimpanzee had been discovered in the Late Tertiary deposits of the Siwalik Hills in N.W. India, and Dubois was of the opinion that there were close faunal connections between Java and India.

Continuing the excavations at Trinil in the following month (September 1891) Dubois obtained from the same deposit the top of a low-vaulted skull with prominent brow-ridges, and this he also regarded at first as belonging to chimpanzee and reported it as such in his quarterly report to the Mining Authority. This specimen was in fact the famous Java Skull (Text-fig. 39).

Resuming excavations at Trinil in the dry season of the following year, Dubois discovered in the same ashy layer a lower premolar tooth (Text-fig. 38, *left*), obviously hominoid, and—fifty feet away from the previous find—a femur (thigh-



FIG. 38. Trinil teeth : premolar (*Pithecanthropus*), molar (*Pongo*). Nat. size.



FIG. 39. Calvaria of *Pithecanthropus erectus*, discovered at Trinil, Java, by Eugene Dubois in 1891. $\times \frac{1}{2}$ nat. size.

bone) which as an anatomist he at once recognized as that of an upright-walking creature. He became convinced, however, that all these specimens belonged to the same species—indeed he thought that they were parts of a single individual. He estimated that when the skull was complete its capacity must have been 908 cc. (*sic!*), whereas in man the cranial capacity rarely if ever fell below 1,000 cc.

Dubois' first scientific account of these important finds appeared in German⁵ in 1894 under the title (translated) "*Pithecanthropus erectus, a Man-like Transitional Form from Java*". The generic name, *Pithecanthropus* (from the Greek *πιθηκος* ape *ἄνθρωπος* man) had already been used by the evolutionist Ernst Haeckel

in 1866⁶ for the hypothetical transition between ape and man, popularly known as the Missing Link. The specific name, *erectus*, referred of course to the inferred upright posture of the creature.

The publication of this paper by Dubois in 1894 naturally gave rise to considerable controversy. There were many points in dispute: did the skull-cap and the thigh-bone belong to the same creature or could the first be ape and the second human? Were they even contemporaneous? What was the geological age of the deposit from which they had been obtained: Pliocene or Pleistocene? One thing at least was certain, Dubois had discovered a skull more human than that of any known ape, and more ape-like than that of any known man.

Further discoveries in Java and in China after the first world war left no doubt that *Pithecanthropus* was an early stage in the evolution of man. Looking back one might count Dubois' discovery as the first concrete proof of man's evolution from an ape-like stock. But the absolute and relative dating of the Javanese material are still matters actively engaging attention.

Dubois at first⁷ regarded the stratum containing the remains of *Pithecanthropus* as of Pleistocene age, but later⁸ he stressed the difficulty of distinguishing between Tertiary and Quaternary faunas in the tropics, which were largely unaffected by the glaciations. After comparing the Trinil fauna with the fossil faunas in North-west India, he eventually came to the conclusion⁹ that it was equivalent to that of the uppermost Siwalik Beds, then regarded as Upper Pliocene.

In the hope of obtaining more evidence about *Pithecanthropus*, particularly in regard to the vital question of its geological age, a German expedition under Frau Selenka visited Java in 1906 and made extensive excavations at Trinil.¹⁰ Although more than 10,000 cubic feet of earth were moved, no further remains of "Java Man" were brought to light. The quantities of associated fossil fauna collected on this expedition helped towards a new assessment of the age of the deposits.

The Trinil beds are partly fluviatile, consisting of clays and sands deposited by the river, but also including quantities of volcanic ejectamenta, mainly ash and *lapilli*. The fossil bones occur in a conglomeratic ashy layer¹¹ two or three feet thick (Text-fig. 40) which appears to have been the result of a tumultuous flood following a volcanic eruption.¹²

The Trinil bone-bed, the horizon of *Pithecanthropus*, yielded remains of a rich mammalian fauna of Asiatic origin: deer, pigs, tapirs, hippopotamus, monkeys, carnivores, and—particularly important from the point of view of dating and correlation—the extinct elephant *Elephas hysudricus*, an advanced form of the elephantine *Stegodon*, and primitive wild cattle known as *Epileptobos*. Blankenhorn, reviewing the palaeontological evidence in 1911, concluded¹³ that the Trinil beds should be ascribed to the "period of transition" marked in Europe by deposits with *Elephas meridionalis*, at that time still regarded by most geologists as Late Pliocene. His collaborator Julius Schuster, on the other hand, pointed out¹⁴ that the fossil plants in a seam of clay in the upper part of the Trinil beds indicated a cooler and wetter climate than at present, which favoured correlation with an early Pleistocene glacial stage. Glacial conditions in high latitudes were probably

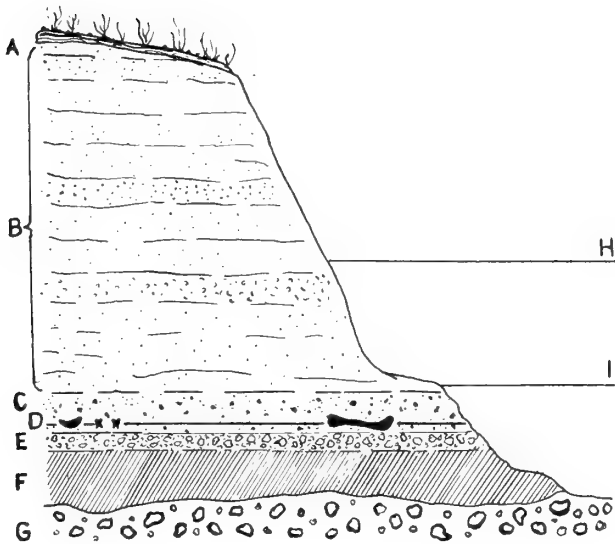


FIG. 40. Section of the deposits at the *Pithecanthropus* site at Trinil, based on drawing by Dubois.

coincident with wetter or "pluvial" conditions in the tropical and equatorial regions.

At about the same time as the members of the Selenka expedition were reporting their findings, the palaeontologist Emil Haug published a very far-sighted solution to the problem of where to draw the boundary between Pliocene and Pleistocene. The practice of defining the Pleistocene as commencing with glaciation was proving useless to geologists working on deposits possibly of this age in regions which had never been glaciated. Haug suggested¹⁵ that the initial spread of true elephant (*Elephas*), true horse (*Equus*) and cattle (*Bos*) should be taken to mark the base of the Pleistocene. This involved including within the period those deposits termed Villafranchian in Europe which contained remains of *Elephas* (*Archidiskodon meridionalis*) or of the co-lateral species *Elephas planifrons*. Although the horse had not reached Java by the time of deposition of the Trinil beds, the presence of *Elephas* and *Epilepotobos* in these layers qualified them for inclusion in the Pleistocene according to Haug's definition, which was not, however, widely accepted until many years later.¹⁶

In a review of the evidence for the age of *Pithecanthropus* published in 1931, Van Es ascribed the Trinil beds to the Lower Pleistocene.¹⁷ The modern practice of classifying the deposits of the Pleistocene period as Lower, Middle or Upper, developed during the second quarter of this century, but apparently without any published agreement as to how or where the boundaries should be drawn.¹⁸ The

species of elephant which successively predominated in Europe (Text-figs. 41-43) served as one of the bases for this subdivision as follows :

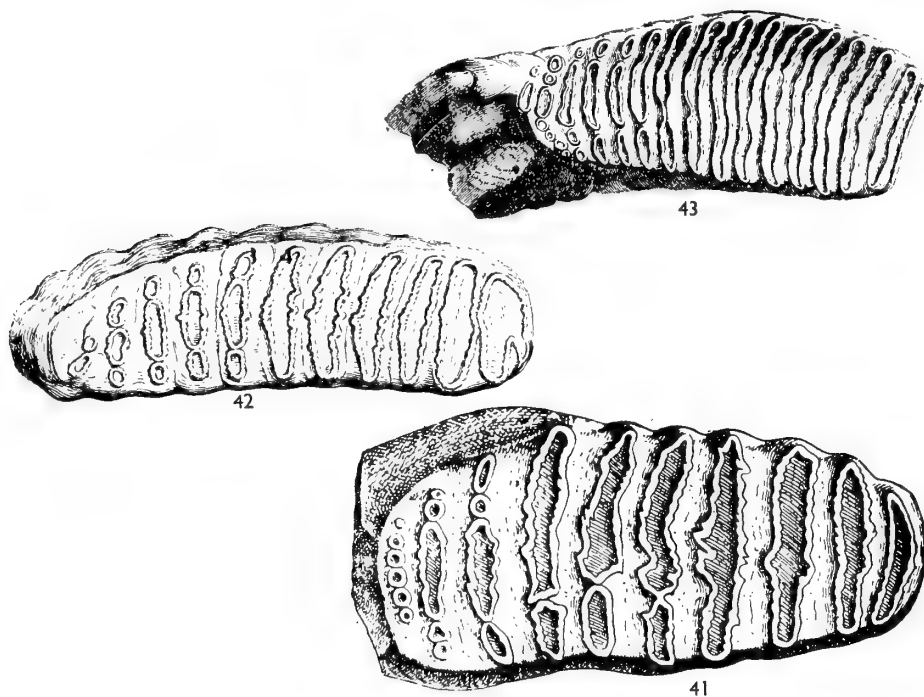
Upper Pleistocene : *Elephas* (*Mammuthus*) *primigenius* (mammoth).

Middle Pleistocene : *Elephas* (*Palaeoloxodon*) *antiquus*.

Lower Pleistocene : *Elephas* (*Archidiskodon*) *meridionalis*.

There is an overlap in the time ranges of these species but the time of first appearance of each serves to mark the base of a division. Attempts have been made to extend this system beyond Europe by correlation of equivalent or co-lateral species. Thus eastwards through Asia *Elephas meridionalis* gave place to *E. planifrons*. In recent years the recognition of *Elephas* (*P.*) *hysudricus* as equivalent to *E. (P.) namadicus* in the Indian Pleistocene, and that in turn as closely comparable with *E. (P.) antiquus* in Europe, has contributed to the modern classification of the Trinil beds as Middle Pleistocene.¹⁹

The next important discovery was made in Europe. Herr J. Rösch, owner of a sand pit at Mauer in the valley of the Neckar, 6½ miles south-east of Heidelberg, had been encouraged by Dr. Otto Schoetensack, geologist in that university, to



FIGS. 41-43. Penultimate lower molars of the three subgenera of *Elephas* which distinguish the main divisions of the Pleistocene.

FIG. 41. *Elephas* (*Archidiskodon*) *meridionalis* Nesti. After Commont. $\times \frac{1}{3}$ nat. size.

FIG. 42. *Elephas* (*Palaeoloxodon*) *antiquus* Falconer & Cautley. After Falconer & Cautley. $\times \frac{1}{3}$ nat. size.

FIG. 43. *Elephas* (*Mammuthus*) *primigenius* Blumenbach. After E. Lartet. $\times \frac{1}{3}$ nat. size.

take an interest in the fossil bones brought to light from time to time during the digging of the sand which was of early Pleistocene age. He had cherished the hope that one day remains of early man would be found. On October 21st 1907 his dream came true.²⁰ One of his workmen unearthed a massive human mandible, obviously fossil, just over 80 feet below the top surface of the deposits (which were worked in terraces), and about 3 feet above their base (Text-fig. 44). The discovery was witnessed by another workman and by a boy. Herr Rösch at once sent word of the discovery to Dr. Schoetensack, who visited the site on the following day.

The Heidelberg jaw (Plate 3) is remarkably complete and well preserved, although the crowns of four of the teeth on the left side adhered to pebbles in the deposit and

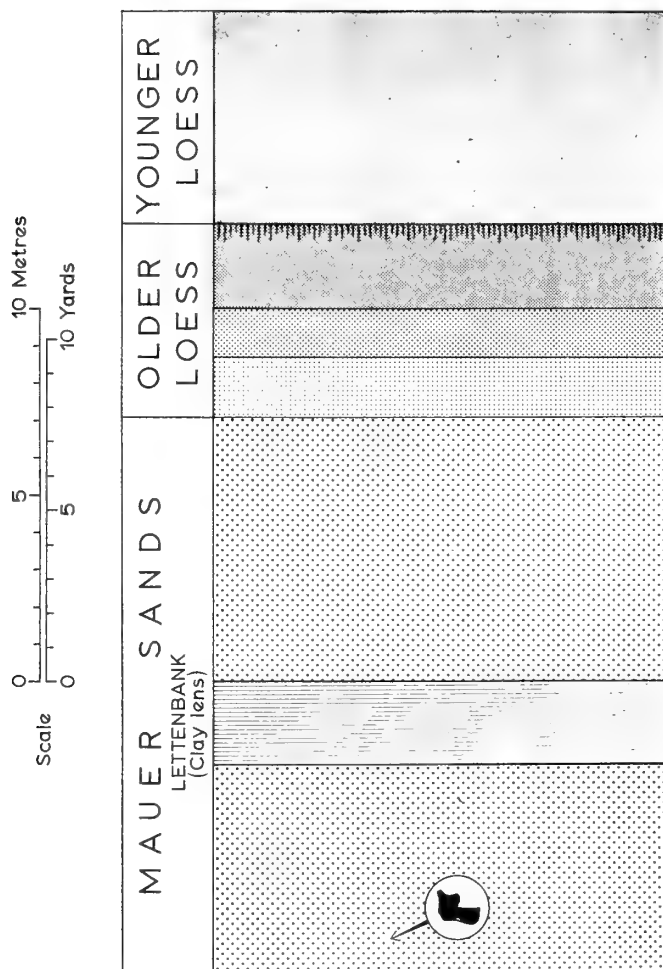


FIG. 44. Section of the Mauer sandpit, near Heidelberg. Scale drawing based on original photograph published by O. Schoetensack (1908).

were lost while it was being dug out. The bone itself, deep yellow in colour and speckled with small black dendrites, is obviously identical in preservation with the numerous fossil mammalian remains found in the Mauer Sands. The jaw gave rise to very little controversy, probably because it was such a thoroughly satisfactory find from many points of view: its stratigraphic position was beyond doubt; it required no restoration; it was extremely "primitive"; unlike the jaw of any living race of man, yet unquestionably human, thus agreeing with evolutionary theory without presenting any problem as to whether it should be classed with man or with apes; and above all it was competently investigated by Schoetensack who lost no time in publishing a comprehensive monograph on the specimen and its geological age.²¹

The associated fauna, indicating a temperate climate and mainly woodland conditions, included *Elephas* (*Palaeoloxodon*) *antiquus*, *Rhinoceros* (*Dicerorhinus*) *etruscus*, *Sus* (pig), *Hippopotamus*, *Bison*, *Cervus elaphus* (red deer), *Equus*, *Trogontherium* (giant beaver), *Castor* (ordinary beaver), *Machairodus* (sabre-tooth cat) and *Ursus arvernensis* (Villafrancian bear).

We may recall that Neanderthal teeth were already known in association with *Elephas* (*Palaeoloxodon*) *antiquus* at Taubach in Eastern Germany, but the presence at Mauer of *Trogontherium*, *Dicerorhinus etruscus* and *Ursus arvernensis*, survivors of the Villafranchian fauna of Europe, indicated that the Heidelberg Man dated from much closer to the beginning of the Pleistocene. No stone artifacts were found in the Mauer Sands, but after comparison with the Pleistocene succession in Belgium, Rutot²² concluded that the horizon of the jaw was earlier than that of the Strepyan and Mesvinian industries, then regarded as Pre-Chellean.

The great antiquity of the Heidelberg jaw was indicated not only by the associated fauna, but also by its stratigraphic position. The Mauer Sands, which were evidently laid down under temperate conditions, are overlain by loesses and loess-loams representing a succession of glacial and interglacial periods. Schoetensack recognized the following sequence:

Younger Loess : 19 feet

Older Loess : 17 feet

Mauer Sands : 43 feet.

Loesses are valuable for Pleistocene correlation because they were formed contemporaneously with glaciation, but are traceable for considerable distances beyond the glaciated region. These dust deposits accumulated under the intensely dry, windy conditions which widely prevailed during glacial stages on account of the anticyclone associated with an ice-sheet; and in north-western Europe they generally contained a calcareous component. During the warmer and moister interglacial periods, when the surface became more thickly vegetated, soil acids percolating downwards gradually converted the loess into loam. Where the loess of one glacial stage overlies that of an earlier one, the junction between them is clearly marked by the zone of loamy weathering at the top of the older. It was soon recognized that the Younger Loess at Mauer was formed during the Last Glaciation, and the Older Loess during the Third or Riss. Thus the underlying sands were at least of Second Interglacial age, and probably older. Rutot²³ considered that a

layer of sandy clay in the middle of the sands represented the Mindel glaciation, a correlation which placed the horizon of the jaw (found near the base of the sands) in the preceding or First Interglacial. Subsequent research showed that this was the correct dating of Heidelberg Man, but Rutot based it on wrong evidence for the sandy clay is merely a facies of the Mauer Sands, not indicating any climatic change.

When the geologist Soergel reinvestigated the sections in the Mauer sand-pit in 1927²⁴ he found that the Younger and Older Loesses were subdivisible by levels of loamy weathering which represented mild intervals (interstadials) within the main glacial stages. He also found evidence of a considerable break in the sequence between the Mauer Sands and the Older Loess of the Riss glaciation. The absence of glacial erratics from the gravel layers within the Mauer Sands has been cited²⁵ as evidence that these deposits of the ancient Neckar river were laid down before they received outwash from the first extensive glaciation, which was the Mindel. Thus, on the basis of stratigraphical geology there seemed little doubt that the Mauer Sands dated from a very early stage of the Pleistocene period. Yet there has been a conspicuous lack of agreement among authorities as to whether the horizon of Heidelberg Man should be counted as Lower Pleistocene, or as Middle Pleistocene. This is more a question of what label to attach to this stratigraphical level, than of doubt as to what level the sands represent (see below).

Professor F. E. Zeuner, following some earlier continental workers, drew the arbitrary line between Lower and Middle at the beginning of the "Great Interglacial" thus including both the Mindel and the Günz glaciations in the Lower Pleistocene.²⁶ This does not correspond with the classification now most widely adopted, that is to say the one based on Haug's proposal (p. 137) which lowered the base of the Lower Pleistocene to include the long preglacial stage known as Villafranchian, formerly classed as Upper Pliocene. The modern classification of the earlier part of the Pleistocene is therefore as follows:—

Middle Pleistocene	{ Mindel-Riss interglacial Mindel glaciation Günz-Mindel interglacial
Lower Pleistocene	{ Günz glaciation ²⁷ Pre-Günz : warm preglacial stages interrupted by minor glacial advances.

The stratigraphical position of the Mauer Sands is well attested by their mammalian fauna. This is fully interglacial in character, of a facies indicating a mixed-oak forest background, and broadly similar to the fauna of the Cromer Forest Bed, recognized by James Geikie as representing the First or Norfolkian Interglacial.

The faunal remains in the Mauer Sands all belong to a contemporaneous group, whereas the "Cromer Forest Bed fauna" appears to contain a mixture of faunas representing several time levels,²⁸ and consequently wide use of the term Cromerian as a faunal stage name needs reconsideration. When the Mauer fauna was compared with other early mammalian assemblages on the Continent its position in the sequence of Pleistocene stages became quite clear.²⁹ It is post-Villafranchian, and therefore no longer classed as Lower Pleistocene. Thus *Elephas meridionalis* (a

species of the subgenus *Archidiskodon*) is absent from the Mauer assemblage while *Elephas antiquus* a species of the subgenus *Palacoloxodon*, typical of the Middle Pleistocene, is present in considerable strength (forming 18 per cent. of the fauna),³⁰ although it is of a primitive form.³¹

The Mauer fauna is younger than the temperate steppe fauna of Mosbach near Mainz, which includes a subspecies of *E. meridionalis* and probably corresponds with the weak Günz glaciation in the Alps ; but it is older than the cool steppe fauna of the Süssenborn gravels in Thuringia which can be equated with the oncoming of the Mindel glaciation. The absence of the cave-hyaena, *Crocota crocuta*, from the Mauer fauna indicates that it antedates the whole Mindel complex.³²

Thus the sands which yielded the Heidelberg jaw are confidently regarded as belonging to the First or Günz-Mindel Interglacial, and not to a Mindel interstadial as suggested until recently by some authorities.

Anatomically among the most notable features of the Heidelberg jaw, are its massiveness and absence of chin. The side wings, known technically as the ascending rami, are only shallowly notched ; and they are exceptionally broad, thus providing an unusually large area for the attachment of the *masseter* muscles used in chewing. This last feature indicates that the lower jaw in this type of man was, as Sir Arthur Keith expressed it³³ "framed to serve the purpose of mastication", whereas "the mandible of modern Man is modified to serve in speech". Relative to the size of the jaw itself the teeth are rather small but very strongly implanted. Their roots are fused, a development which may be connected with powerful mastication. As in the lower jaw of Neanderthal men, the place of the tubercle in the inside of the chin region which in modern man serves for attachment of tongue muscles is occupied by a small pit.

Schoetensack referred the jaw to an extinct species of mankind, *Homo heidelbergensis*, which became regarded by many anthropologists as the precursor of *Homo neanderthalensis*. However, a number of authorities have questioned whether the species represented by this jaw should be placed in the same genus as the Neanderthal and modern species of man (i.e. in *Homo*). W. H. L. Duckworth,³⁴ for instance, said : "Would the Mauer jaw be appropriate to the cranium of *Pithecanthropus*? I believe an affirmative answer is justified". The view is now widely held that Heidelberg Man was in all probability the European equivalent of *Pithecanthropus*, but until a cranium of the former is known generic identification must remain in doubt.

Historically it is interesting to read what Keith³⁵ had to say about "*Homo heidelbergensis*" in 1911 : "From the Heidelberg jaw", he wrote, "we learn that the human mechanism of mastication was fully evolved at the beginning of the Pleistocene Period. The canine teeth which are so large and prominent in all forms of anthropoids have in the Heidelberg specimen subsided to the level of the neighbouring teeth in the dental series. We must assume that at one period in the evolution of Man the canines were prominent and pointed as in the anthropoids. . . . The retrogression of the canine teeth in the primitive human stock and the evolution from the anthropoid . . . must be sought for in the Pliocene period or even earlier."

It is clear from these remarks that the Pliocene ancestor of man was expected to have a more ape-like lower jaw than the early Pleistocene Man of Heidelberg. At about the same time that Keith was expressing this opinion, another anatomist, Elliot Smith,³⁶ had made out a strong case for believing that in the evolution of man "the brain led the way". It was therefore not unreasonable to believe that the hypothetical ape-jawed ancestor living in the Pliocene period would have had a braincase that was manifestly human—indeed perhaps more human in appearance than the braincase of *Pithecanthropus* which was still regarded by some authorities at that time as an ape.³⁷

It is not unlikely that against this background of ideas, the amateur archaeologist Charles Dawson began to entertain the hope that some of the ancient gravels in his own county of Sussex would one day yield relics of man's Pliocene ancestor. Already in 1899³⁸ he had noticed a patch of gravel at Piltdown near Fletching which he thought was a possible source of fossils. The gravel contained eoliths, supposed by some to be artifacts of Pliocene Man. Whether it was Dawson, or one of his acquaintances, who first thought that this would be an excellent finding-place for a fabricated "missing link" we may never know, but in due course this idea bore fruit in the form of "*Eoanthropus*".

SECTION VI (Notes)

- ¹ DUBOIS, E. 1889. On the need for an investigation into the existence of the Ice Age fauna in the Dutch East Indies, especially in Sumatra. *Natuurk. Tijdschr. Ned.-Ind.*, Batavia, **48** : 148-163. (In Dutch.)
- ² For a general account of the Javanese discoveries see Koenigswald, G. H. R. von. 1956. *Meeting Prehistoric Man* : 20-39, 65-142. London.
- ³ Dubois first reported the Kedung Brubus and Trinil finds in the quarterly reports to the Mining Authority : *Verslagen van het Mijnwезen*, 4de Kwartaal, 1890 ; 3de Kwartaal, 1891 ; 4de Kwartaal, 1891 ; 3de Kwartaal, 1892 ; 4de Kwartaal, 1893.
- ⁴ Described by Lydekker, R. (1886 *Palaeont. indica.*, Calcutta (10) **4** : 2) as *Troglodytes sivalensis*, later referred to *Sivapithecus* Pilgrim (1915 *New Siwalik Primates and their bearing on the Question of the Evolution of Man and the Anthropeidea*. *Rec. Geol. Surv. India*, Calcutta, **45** : 1-74 (esp. p. 47).
- ⁵ DUBOIS, E. 1894. *Pithecanthropus erectus, eine menschenähnliche Ubergangsform aus Java*. Batavia. Also in *Jaarb. Mijnw. Ned.-Oost-Ind.*, Buitenzorg, **1895** : 5-77.
- ⁶ HAECKEL, E. 1875. *History of Creation* : 3rd ed. 1883, : 271, 293. London.
- ⁷ DUBOIS, E. 1892. *Natuurk. Tijdschr. Ned.-Ind.*, Batavia, **51** : 93-100.
- ⁸ KOENIGSWALD, G. H. R. VON. 1956. *Meeting Prehistoric Man* : 38, 39. London.
- ⁹ DUBOIS, E. 1908. Das geologische Alter der Kendeng oder Trinilfauna. *Tijdschr. K. Ned. Aard. Genoot.*, Amsterdam, **25** : 1235-1270.
- ¹⁰ SELENKA, L. & BLANCKENHORN, M. 1911. *Die Pithecanthropus-Schichten auf Java*. Leipzig.
- ¹¹ DUBOIS, E. 1896. On *Pithecanthropus erectus* : a transitional form between Man and Apes. *J. Anthropol. Inst.*, London, **25** : 240-255.
- ¹² TERRA, H. DE. 1943. Pleistocene Geology and Early Man in Java. *Trans. Amer. Phil. Soc.*, Philadelphia (n.s.) **32** : 447-450.
- ¹³ BLANCKENHORN, M. In Selenka, L. & Blanckenhorn, M. 1911 : 264-265. See Note 10.
- ¹⁴ SCHUSTER, J. 1911. In Selenka, L. & Blanckenhorn, M. 1911 : 219, 256. See Note 10.
- ¹⁵ HAUG, E. 1911. *Traité de Géologie*, **2** : 1767. Paris. Haug pointed out that new types of Asiatic origin appeared abruptly in the Villafranchian stage : "ces immigrants sont les

- genres *Elephas*, *Equus* et *Bos*. Leur introduction soudaine dans la faune européenne constitue un événement assez important pour justifier l'établissement d'une coupure de premier ordre. Aussi placerons-nous à la base du Quaternaire le Villafranchien".
- ¹⁶ The Pliocene-Pleistocene Boundary (ed. K. P. Oakley), *Rep. 18th Sess. Int. Géol. Congr.* (London, 1948), Pt. ix, 1950 : 6.
 - ¹⁷ ES, L. J. C. VAN. 1931. The Age of *Pithecanthropus* : 134-137. The Hague.
 - ¹⁸ KOENIGSWALD, G. H. R. VON. 1956. *Meeting Prehistoric Man*, London ; HOOIJER, D. A. 1956. The lower boundary of the Pleistocene in Java and the age of *Pithecanthropus*. *Quaternaria*, Rome, **3** : 5-10.
 - ¹⁹ HOPWOOD, A. T. 1935. Fossil Elephants and Man. *Proc. Geol. Ass., Lond.*, **46** : 55. SOERGEL, W. 1913. *Elephas trogantherii* Pohlig und *Elephas antiquus* Falc. *Palaeontographica*, Stuttgart, **60** : 799.
 - ²⁰ KEITH, A. 1925. *The Antiquity of Man*, **1** : 319.
 - ²¹ SCHOETENSACK, O. 1908. *Der Unterkiefer des Homo heidelbergensis : Ein Beitrag zur Palaeontologie des Menschen*. Leipzig.
 - ²² RUTOT, A. 1909. Note sur la Mâchoire humaine de Mauer. *Bull. Soc. Belge Géol. Pal. Hydr.*, Bruxelles, **22** : 117-132. Referred the Lower Mauer Sands, which yielded the jaw, to the horizon of the "Mafflian" flake industry, which he then regarded as Pre-Chellean but later equated with Chellean (see Sollas, W. S. 1924. *Ancient Hunters* : 156, 174. 3rd ed. London).
 - ²³ RUTOT, A. (1909 : 131) termed the clayey layer between the Lower and Upper Mauer Sands the *Lettenbank* and equated it with the *Glaise moséene* in Belgium which was then considered to be contemporaneous with a phase of the Mindel glaciation.
 - ²⁴ SOERGEL, W. 1928. Das geologische Alter des *Homo heidelbergensis*. *Paläont. Z.*, Berlin, **10** : 217-233. See also Zeuner, F. E. 1958. *Dating the Past* : 156. 4th ed. London.
 - ²⁵ HOWELL, F. C. 1960. European and Northwest African Middle Pleistocene Hominids. *Curr. Anthropol.*, London, **1** : 199-202.
 - ²⁶ ZEUNER, F. E. 1958. *Dating the Past* : 118. 4th ed. London.
 - ²⁷ OAKLEY, K. P. 1961. The Günz Glaciation. *New Scientist*, London, **11** : 246. A few authors count the Günz glacial stages as the base of the Middle Pleistocene, but Günz-stage deposits on the south side of the Alps contain Villafranchian fauna according to Nangeroni (1950) and Venzo (1955) quoted by Flint, R. F. 1957. *Glacial and Pleistocene Geology* : 384-387. London.
 - ²⁸ AZZAROLI, A. 1953. The Deer of the Weybourne Crag and Forest Bed of Norfolk. *Bull. Brit. Mus. (Nat. Hist.) Geol.*, London, **2** : 90.
 - ²⁹ HOWELL, F. C. 1960. European and Northwest African Middle Pleistocene Hominids. *Curr. Anthropol.*, London, **1** : 199-202.
 - ³⁰ SOERGEL, W. 1923. Die diluvialen Säugetiere Badens I. *Mitt. bad. geol. Landesanst.*, Heidelberg, **9** : 1-254 (esp. p. 173).
 - ³¹ ADAM, K. D. 1961. Die Bedeutung der Pleistozänen Säugetier-Faunen Mitteleuropas für die Geschichte des Eiszeitalters. *Stuttgart. Beitr. Naturh.*, **78**.
 - ³² In contrast the Corton beds, which probably represent a Mindel interstadial, do contain teeth of *Crocota crocuta*. Kurtén, B. 1956. The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. *Amer. Mus. Novit.*, New York, 1764 : 41.
 - ³³ KEITH, A. 1911. *Ancient Types of Man* : 83. London.
 - ³⁴ DUCKWORTH, W. H. L. 1912. *Prehistoric Man* : 14. Cambridge.
 - ³⁵ KEITH, A. 1911 : 84.
 - ³⁶ SMITH, G. ELLIOT. 1913. *Rep. Brit. Ass.*, **1912** : 594-598 ; 1927. *Essays on the Evolution of Man* : 71. 2nd ed. Oxford.
 - ³⁷ SMITH, G. ELLIOT. 1927 : 71.
 - ³⁸ DAWSON, C. 1913. The Piltdown Skull. *Hastings Nat.*, **2** : 75-76.

VII. PRINCIPLES OF RELATIVE AND ABSOLUTE DATING

The chronological placing of fossils, whether they be early men or lower organisms, is fundamentally important for understanding their evolutionary relationships. Several distinct kinds of dating are involved. *Relative dating* places an event with reference to some other event in a time-sequence. A fossil or a deposit can be regarded as representing an "event": the interval of time when it was alive or being formed. In the relative dating of fossils reference is generally made to irregularly spaced, arbitrarily chosen events, which are geological, palaeontological or archaeological. For example, in Europe the spread of *Elephas*, *Equus* and *Bos* has been chosen to mark the beginning of Pleistocene time, the ending of glacial conditions to mark the beginning of Recent, Post-Glacial or Holocene time, and the change from hunting to farming economy to mark the beginning of the Neolithic period. In the sense that none of these events occurred everywhere simultaneously, the dating of a specimen as Basal Pleistocene, Early Post-Glacial or Early Neolithic does not necessarily imply exact contemporaneity with specimens similarly dated in other parts of the world.

All dating is in a sense "relative", but when it relates an event to a regular astronomical event-series, particularly the passage of years or sidereal time, it is commonly called *absolute dating*. Thus, to date a skull as "Early Neolithic" is to place it in a sequence of archaeologically determined events; to date it as 6000 B.C. is to date it absolutely. Unfortunately the use of the term "absolute dating" as synonymous with "dating in years" has blunted the meaning of the word absolute, for it makes no distinction between referring an event to a span of years and referring it to a particular instant in time. Some authors¹ have preferred to use the term "absolute" age with reference to contemporaneity between one deposit or species and another. For instance, if two deposits in widely separated regions were proved to be contemporaneous without being dated in years they could be said to be of the same absolute age. On the other hand, two deposits both dated as being "between 20,000 and 25,000 years old" (so-called absolute dating) might not be contemporaneous. In such cases relative dating may be more informative.

To know the correct time sequence of the fossil remains of man and his ancestors is basic to interpreting their significance; but it is equally important from the point of view of understanding evolutionary process to obtain a measure of how much time separates one form from another. We are therefore concerned with two main classes of dating:

Relative Dating: the stratigraphical or archaeological age of a specimen or formation.

Chronometric Dating (hitherto called Absolute Dating):² the age of a specimen or formation measured in years.

In practice there are several kinds of relative dating, each depending on a different range of evidence. When a human skull, for example, is dug up in some ancient deposit, those concerned with the discovery usually enquire at once: "Is it reliably dated?" The first question to be settled is whether the specimen is contemporaneous with the deposit in which it was found, or whether it has been intrusively buried, or

whether (as sometimes happens) it has been derived from some older formation and redeposited. This primary dating, the age-relation of a specimen to its containing deposit and to the associated finds, may be termed for convenience R.1 or first-order relative dating. If the specimen is a bone (or tooth) determination of its chemical composition in comparison with that of other bones of known stratigraphical age in the same deposit is a valuable means of establishing whether it is contemporaneous, intrusive or derived, for the chemical composition of buried bones changes in course of time. The analytical methods of dating bones, including fluorine analysis, nitrogen analysis and radiometric assay,³ are mainly used for R.1 dating which is particularly important in connection with supposedly fossil human remains because of man's long-established habit of burying the dead.

When a scientific excavator discovers human remains, one of his first concerns naturally is to look for evidence showing whether they were artificially interred, or whether they were deposited or incorporated in some way during the accumulation of the containing deposit ; but the evidence in this respect is sometimes rather unclear. It may be lacking altogether if the human remains were removed from the ground in the absence of an experienced excavator, or if they were discovered in days before scientific methods of archaeological excavation had been introduced. Consequently, analytical methods of confirming or establishing the R.1 dating, that is to say whether human bones from ancient deposits are contemporaneous or non-contemporaneous with bones of known stratigraphical age from the same site, are useful both as a routine procedure and as a means of re-evaluating some of the early discoveries.

We may recall that it was the R.1 dating that was in doubt in all the following discoveries of possibly early remains of *Homo sapiens* :

Gailenreuth (1771) : Were the human bones contemporaneous with the associated cave-bear? (p. 92).

Paviland (1823) : Was the human skeleton contemporaneous with the associated mammoth remains, or a later burial? (p. 89, 106).

Grotte de Bize (1830) : Were the human bones contemporaneous with the associated extinct animals? (p. 91).

Aurignac (1852) : Were any of the human bones contemporaneous with the nearby Upper Palaeolithic fauna, or did they all belong to the superimposed burials of Neolithic age ? (p.106).

Moulin-Quignon (1863) : Was the human jawbone contemporaneous with the high-terrace gravel (containing "Chellean" *haches* or hand-axes) in which it was found, or was it a later implantation ? (p. 111ff).

Calaveras (1866) : Was the human skull contemporaneous with the Pliocene bone-bed in which it was allegedly found, or had it been recently implanted ? (p. 120f).

Foxhall (1855) : Was the human jawbone contemporaneous with the "Pliocene" (now classed as Lower Pleistocene) marine formation in which it was embedded, or was it part of a later burial ? (p. 118f).

Cro-Magnon (1868) : During the last century a few authorities doubted

whether the interments in this cave were contemporaneous with the closely associated Upper Palaeolithic fauna, and suggested that they were early *post*-Palaeolithic (p. 123).

Castenedolo (1880, following an unpublished find of 1860) : Were the four skeletons contemporaneous with the Pliocene marine clay in which they were found (a Pliocene shipwreck was seriously suggested !) or were they in Post-Pliocene graves ? (p. 118).

Galley Hill (1888) : Was the human skeleton contemporaneous with the Middle Pleistocene gravel (containing Acheulian hand-axes) in which it was found, or was it an intrusive burial of much later date ? (p. 131).

In many of the other discoveries of early human or pre-human remains which we have reviewed there was no reason to doubt their contemporaneity with the deposit in which they were found but the stratigraphical or archaeological age of that deposit constituted a problem. The stage in the local stratigraphical sequence to which the containing deposit (or contemporaneous fauna or culture) is referable may be called the *R.2 dating* of a specimen. The inferred position of that stage in terms of world or wider-scale stratigraphy or culture sequence may be called *R.3 dating*. The distinction between *R.2* and *R.3* dating is rather arbitrary, but the former is usually based on fact, the latter on inference. There are of course some cases where *R.2* dating and *R.3* dating are synonymous. The following examples serve to illustrate the distinction between the various orders of relative dating :

	R.1*	R.2	R.3
Engis I skull (1830) . . .	<i>c.</i>	" Cold " Mousterian	Würm I
Engis II skull (1830) . . .	<i>c.</i>	Aurignacian	Würm interstadial
Neanderthal skeleton (1856) . . .	<i>c.?</i>	No direct evidence	No direct evidence
Cro-Magnon skeletons (1868) . . .	<i>a.c.</i>	Aurignacian	Würm
Galley Hill skeleton (1888) . . .	<i>i.</i>	Post-Swanscombe Middle Gravels	Post-Pleistocene or End-Pleistocene?
Gibraltar I skull (1848) . . .	<i>c.?</i>	No direct evidence	No direct evidence
Gibraltar II skull (1926) . . .	<i>c.</i>	Upper Mousterian	Würm
Spy skeletons (1886) . . .	<i>a.c.</i>	" Cold " Mousterian	Würm I
Trinil skull (1891) . . .	<i>c.</i>	Trinil Beds	Middle Pleistocene
Taubach tooth (1887) . . .	<i>c.</i>	" Warm " Mousterian	Riss-Würm
Heidelberg jaw (1907) . . .	<i>c.</i>	Mauer Sands	Günz-Mindel
Weimar-Ehringsdorf skeletons (1908)	<i>c.</i>	" Warm " Mousterian	Riss-Würm

* Four *R.1* categories are recognized :

c. —contemporaneous with deposit

a.c.—approximately contemporaneous, e.g. Upper Palaeolithic interment in an Upper Palaeolithic deposit.

i. —intrusive burial of much later date than the deposit.

d. —derived from an older formation and redeposited.

When a fossil bone or tooth (or indeed any fossil) is found in isolation, unaccompanied by other organic remains serving to establish the *R.2* or *R.3* age, it can sometimes be dated by its form or morphology. This method of relative dating (which elsewhere I have termed *R.4* dating) is reliable in some groups of fossils where the time-spans of the genera and species are relatively short and well known,

but in other groups, particularly rare groups, it is very unreliable. It does not allow for unsuspected survivals. For example, before the discovery of a living *Coelacanth* in 1938 any new fossil member of this group in rock of unknown age would have been dated morphologically as " unquestionably Cretaceous or earlier ", whereas in fact, as we now know, it might be Tertiary or even Quaternary. Morphological dating of fossil Primates (the group which includes man) has also proved unreliable, but it will no doubt become less so with the increase of our knowledge of the group. Few human palaeontologists would seriously question the correctness of inferring that the Neanderthal and Gibraltar skulls were of Upper Pleistocene age in view of their detailed similarity to the well-dated skulls of Spy, Le Moustier and elsewhere in Europe.

Morphological evidence is usually taken into consideration with other evidence bearing on the antiquity of fossil human remains of doubtful antiquity. Thus if a human skull is found in any early Pleistocene deposit and fails to pass any of the analytical tests for antiquity, the fact of its being indistinguishable from *Homo sapiens* would be regarded by most anthropologists as in keeping with the results of the tests ; whereas if a skull found in similar circumstances were morphologically " archaic ", negative evidence of antiquity would be less convincing.

Establishing the R.2 and probable R.3 ages of human remains depends on the application of the usual methods of stratigraphical geology and archaeology : observation of the stratification of the site where the remains have been found, noting any associated fauna, plant remains and artifacts, and comparing these with the contents of underlying and overlying deposits ; and eventually comparing the sequence with that at other sites further afield. The modern excavator pays particular attention to collecting shells and charcoal from the deposits under investigation, because these are not only likely to provide evidence of the climate prevailing when a deposit was being formed, but if found in sufficient quantities these materials can be chronometrically dated by the radiocarbon method. The excavator also usually preserves samples of the deposits for mineral- and pollen-grain analysis, techniques which provide valuable evidence for relative dating of human remains at some sites.

In many parts of the world the sequence of land faunas through Tertiary and Quaternary times has been worked out in some detail, so that if a large assemblage of contemporaneous mammalian remains is found in association with a fossil human skeleton, or part of a skeleton, its stratigraphical age (R.2 or R.3 dating) is fairly easily determined within certain limits. Fossil invertebrates are also useful for this type of dating, but they are less useful than vertebrate material because contemporaneity cannot be established by analysis. Assemblages of molluscan shells sometimes provide valuable indications of the age of lake beds, river beds and aeolian or other terrestrial deposits. Land and freshwater mollusca are fairly sensitive climatic indicators, and therefore may show whether a deposit is periglacial, interglacial, interstadial or post-glacial. Many of the species have restricted time-ranges (either locally or universally). To mention one example : the land snail *Pomatias elegans* was excessively rare in Britain before Post-Glacial times, and therefore the

discovery that it was abundantly associated with the skeleton of Halling Man led to a revision of the dating of those remains.⁴

In discussing the relative dating of fossil human remains in any detail, it is necessary to be familiar with current terms and methods of classifying and correlating Quaternary deposits.

The "Absolute" or Chronometric dating of early human remains or other fossil bones is of four main types :

A.1 : direct determination of the age of the specimen itself from internal evidence ; for example by measuring the carbon-14 radioactivity of a sample of the bone.

A.2 : direct determination of the age of the source deposit ; for example by measuring the potassium-argon ratio if the deposit is potassic, or by measuring the carbon-14 radioactivity of associated bones, shells or charcoal, or of peaty material from the deposit which contained the specimen in question.

A.3 : the age of a specimen in years inferred by correlation of the source bed (or its horizon) with a deposit whose actual age has been determined.

A.4 : the age in years inferred from some theoretical consideration ; for example dates obtained by expressing the local geological sequence in terms of climatic fluctuations, and matching these with the curve of past insolation as calculated by Milankovitch (the Absolute Chronology of Zeuner).⁵ A more reliable form of A.4 dating recently introduced is the matching of climatic fluctuations in the Pleistocene sequences on land with marine palaeo-temperature changes recorded in ocean bed cores, and dating key layers of sediment in these cores by analysis of their content of uranium daughter elements.

It will be obvious that the validity of A.2, A.3 or A.4 dating of a specimen is conditional on the contemporaneity of the specimen with the containing deposit (i.e. the R.1 dating) being assured. Recent studies have emphasized that attempts at chronometric dating (excluding the A.1 type) are really a waste of time unless the R.1 dating has been established beyond doubt. This is illustrated by a list of the recorded datings of the Piltdown cranium :

1935 attempt at R.1 dating : " Derived from a somewhat older deposit ".⁶
Consequent A.4 dating : *c.* 500,000 years.

1949 revised R.1 dating : " Contemporaneous with latest rearrangement of the deposit ".⁷ Consequent A.4 dating : *c.* 50,000 years.

1953-4 corrected R.1 dating : " Recently implanted " [after being brought from some other site].

Attempted A.4 dating based on preservation of the bone : " Perhaps two or three thousand years old ".⁸

1959 C14 measurement gave chronometric age of the bone (A.1 dating) as :
" A few centuries old ".⁹

The framework of relative chronology for Pleistocene deposits in Europe, Asia and Africa has become more dependable in recent years as a result of key points being dated chronometrically. Already by 1957 more than 120 samples of Upper Pleistocene deposits in Europe had been dated by the carbon-14 method ¹⁰ (limited to the last 60,000 years). Since 1958 the potassium-argon method of chronometric

dating¹¹ has been applied successfully to numerous Lower and Middle Pleistocene volcanic deposits in Africa, Asia, Europe and America. Thus in the future, so long as their relative ages (R.1, R.2, and R.3) are well established, the majority of fossil human remains will be quite reliably dated in years by the A.3 procedure, and in many cases even more closely by the A.2 procedure.¹²

In order to complete this review of the history of human palaeontology, the following annotated table gives the modern chronometric ("absolute") dating of those fossil men whose relative dating has been outlined on p. 147.

Engis I skull. 45-70,000 years B.P.

Engis II skull. c. 30,000 years B.P.

Neanderthal skeleton. 35-70,000 years B.P. (?)

Cro-Magnon skeleton. c. 30,000 years B.P.

Galley Hill skeleton. $3,310 \pm 150$ years B.P.
(1960).

Gibraltar I skull. 45-70,000 years B.P.

Gibraltar II skull. > 30,000 years B.P.
(probably c. 50,000).

Spy skeletons. 45-70,000 years B.P.

Trinil skull. > 500,000 years B.P.

Taubach teeth. 60-120,000 years B.P.?

Heidelberg jaw. > 400,000 years B.P.

Weimar-Ehringsdorf skeletons. 60-120,000
years B.P.

A.3 dating. Cold Mousterian¹³ judged to be in this time bracket on basis of chronometric dating of deposits of Early Würm stage.

A.3 dating. Aurignacian¹⁴s.s. II dated by C14 at La Quina as 31,000 years B.P.

A.4 dating. No associated fauna or artifacts.¹⁵ On *hypothetical* basis of morphology, this type specimen is presumed to be one of the later members of the Neanderthal group; if so, Early Würm or Göttweiger Interstadial in age.

A.3 dating. Aurignacian s.s. i.e. dating on same basis¹⁶ as Engis II skull.

A.1 dating. Fragments of the humeri were directly dated by C14.¹⁷

A.3 dating. Mousterian deposits in caves at Gibraltar judged to date from Early Würm time. Cf. Engis I skull.

A.2/3 dating. Small fragment of charcoal from Upper Mousterian layer at Gib. II site showed no measurable activity (> 30,000 years).¹⁸ Charcoal from about same horizon at nearby site gave C14 age of 48,000 years B.P. (1959).¹⁹

A.3 dating. Same basis as Engis I and Gibraltar I.²⁰

A.3 dating. Potassium-argon age of tektites associated with beds containing Trinil fauna.²¹

A.3 dating. Riss-Würm interglacial²² deposits, as stratigraphically dated by fauna; same age as those of Ehringsdorf (see below).

A.4 dating. Potassium-argon age of volcanic tuffs (c. 400,000 B.P.)²³ linked with Rhine terrace post-dating Mauer Sands, Heidelberg.

A.2 dating. Ratio of uranium daughter elements thorium-protoactinium in interbedded tufa or travertine indicated an age within this bracket.²⁴ This agrees with the Early Neanderthals of Taubach and Ehringsdorf being of Riss-Würm age.

SECTION VII (Notes)

- ¹ EWER, R. F. 1956. The Fossil Carnivores of the Transvaal Caves : Two New Viverrids, together with some general considerations. *Proc. Zool. Soc. Lond.*, **126** : 259-274 (esp. p. 271).
- ² OAKLEY, K. P. 1953. Dating Human Fossil Remains. In Kroeber, A. L. *Anthropology Today* : 43-56. Chicago University Press.
Eight types of dating were distinguished as in the present work ; "Absolute" (in the sense now called Chronometric) : A.1, A.2, A.3, A.4 ; Relative : R.1, R.2, R.3, and R.4.
- ³ OAKLEY, K. P. 1963. Analytical Methods of Dating Bone. In Brothwell, D. & Higgs, E. S. *Science in Archaeology* : 24-34. London.
For practical details of these tests see Oakley, K. P. 1963. Fluorine, Uranium and Nitrogen Dating of Bone. In *The Scientist and Archaeology*. Ed. E. Pyddoke. London.
- ⁴ OAKLEY, K. P. 1963. Note on the antiquity of Halling Man. In Kerney, M. P. Late Glacial deposits on the Chalk of Southeast England. *Phil. Trans. Roy. Soc. Lond.*, ser. B, **246** : 250-251.
- ⁵ ZEUNER, F. E. 1958. *Dating the Past* : 110. 4th ed. London.
- ⁶ HOPWOOD, A. T. 1935. Fossil Elephants and Man. *Proc. Geol. Ass. Lond.*, **46** : 47-50.
- ⁷ OAKLEY, K. P. 1950. On the fluorine test for determining the relative antiquity of fossil bones. *Quart. J. Geol. Soc. Lond.*, **106** : iii. The estimate of 50,000 years appeared in *The Times*, Sept. 6, 1949, the following preliminary report of the results of the fluorine test.
- ⁸ OAKLEY, K. P. 1954. Solving the Piltdown Problem. *Arch. News Letter*, London, **5** : 125.
- ⁹ This carbon-14 dating of a sample of the Piltdown cranium was undertaken in 1959 by the late Professor Hl. de Vries. See Vries, Hl. de & Oakley, K. P. 1959. Radiocarbon Dating of the Piltdown Skull and Jaw. *Nature, Lond.*, **184** : 224-226.
- ¹⁰ LIBBY, W. F. 1955. Radiocarbon Dating. 2nd ed. Chicago. For application of carbon-14 dates to Upper Pleistocene chronology see Gross, H. 1958. *Eiszeiten u. Gegenwart*, **9** : 155-187.
- ¹¹ EVERNDEN, J. F., CURTIS, G. H. & KISTLER, R. 1958. Potassium-Argon dating of Pleistocene Volcanics. *Quaternaria*, Rome, **4** (1957) : 13-17.
- ¹² Thus for example the East African australopithecine "*Zinjanthropus*" has been dated chronometrically by applying the potassium-argon method to the deposit in which it was embedded. See Leakey, L. S. B., Evernden, J. F. & Curtis, G. H. 1961. *Nature, Lond.*, **191** : 478-479. The validity of the date obtained has been widely debated, but it is agreed to be of the order of magnitude of one million years.
- ¹³ TWIESSELMANN, F. 1952. In Catalogue des Hommes Fossiles. *C. R. XIXe Congr. Géol. Int.*, (5) Algiers : 37, Engis I.
- ¹⁴ TWIESSELMANN, F. 1952 : Engis II.
- ¹⁵ GIESELER, W. 1952. In Catalogue des Hommes Fossiles. *C. R. XIXe Congr. Géol. Int.*, Algiers (5) : 19-20. See also Campbell, B. 1956. *Man*, London, **56** : 156-158, 171-173.
- ¹⁶ VALLOIS, H. 1952. In Catalogue des Hommes Fossiles. *C. R. XIXe Congr. Géol. Int.*, Algiers (5) : 74. "Aurignacian (niveau des pointes à base fendue)".
- ¹⁷ BARKER, H. & MACKEY, J. 1961. British Museum Radiocarbon Measurements III. *Radiocarbon*, London, **3** : 41.
- ¹⁸ VOGEL, J. C. to OAKLEY, K. P. *in lit.* Jan. 8, 1962.
- ¹⁹ Charcoal from Upper Mousterian Layer G in Gorham's cave, Gibraltar, was radiocarbon dated by the late Professor H. de Vries in 1958 as c. 48,000 years old.
- ²⁰ TWIESSELMANN, F. 1952. In Catalogue des Hommes Fossiles. *C. R. XIXe Congr. Géol. Int.*, Algiers (5) : 99.
- ²¹ KOENIGSWALD, G. H. R. VON. 1962. Das absolute Alter des *Pithecanthropus erectus* Dubois. *Evolution und Hominisation* : 112-119 (esp. p. 117). Ed. G. Kurth. Stuttgart.
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PLATE I

The Gibraltar I Skull. $\times \frac{1}{3}$ nat. size. Brit. Mus. (Nat. Hist.) ; Royal College of Surgeons'
Collection F.C.2787.

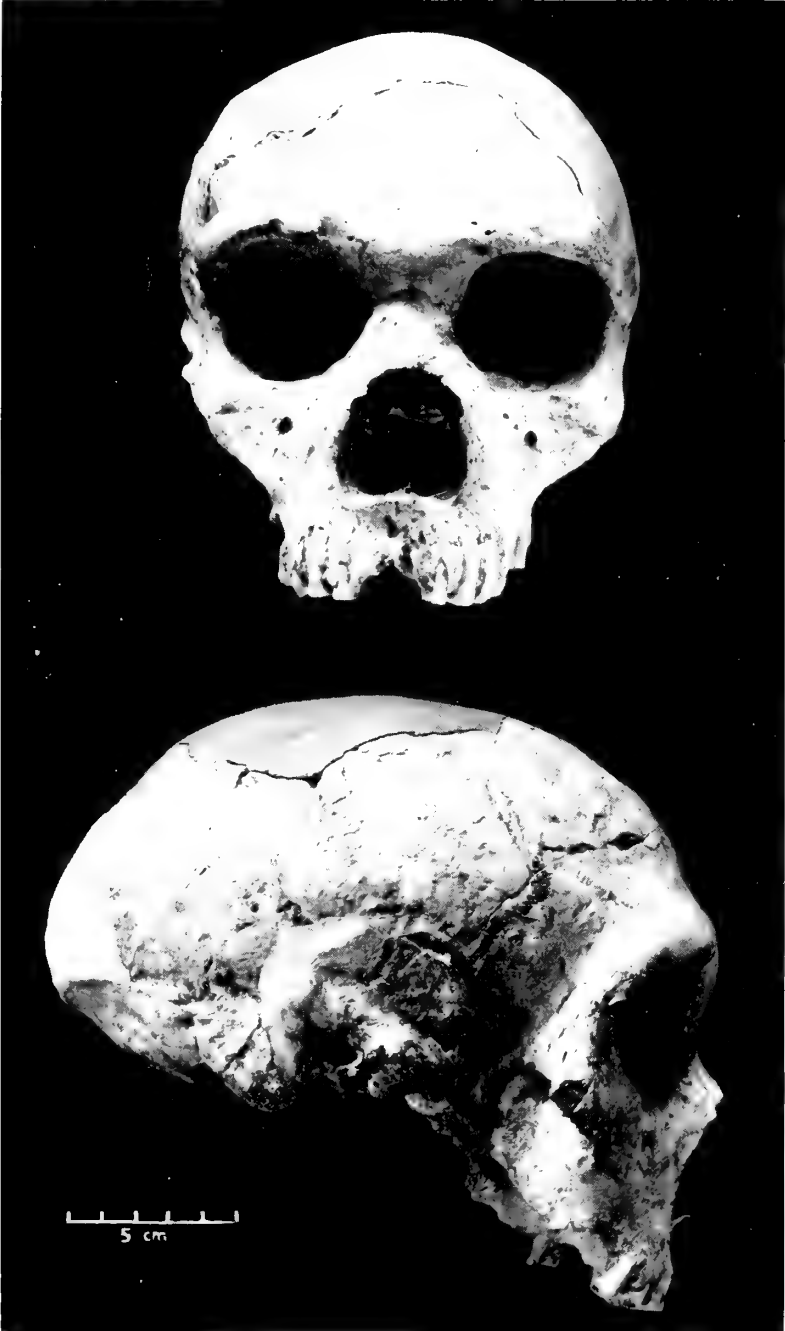


PLATE 2

Cro-Magnon I Skull ("Old Man"). $\times \frac{1}{3}$ nat. size. Musée de l'Homme, Paris. *After*
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PLATE 3

Heidelberg mandible. Two aspects. $\times \frac{1}{3}$ nat. size. Heidelberg University, Germany.
After Schoetensack.





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THE FAUNA OF THE
PORTRANE LIMESTONE, II



A. D. WRIGHT

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THE FAUNA OF THE PORTRANE LIMESTONE, II



BY

ANTHONY DAVID WRIGHT, Ph.D.

(Queen's University, Belfast)

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By A. D. WRIGHT

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SYNOPSIS

This paper is the second of a series by several authors on the Portrane Limestone fauna, and is concerned with the articulate brachiopods of the "*Orthis*" group, comprising the superfamilies Orthacea, Dalmanellacea, Clitambonitacea and Triplesiacea. Thirty-five species belonging to thirty genera are described, including the new family Saukrodictyidae; three new genera, *Portranella*, *Spinorthis* and *Saukrodictya*; sixteen new species and three new subspecies.

I SYSTEMATIC DESCRIPTIONS

Superfamily **ORTHACEA** Woodward 1852

Family **ORTHIDAE** Woodward 1852

Subfamily **ORTHINAE** Woodward 1852

Genus **ORTHAMBONITES** Pander 1830

Orthambonites humilidorsatus sp. nov.

(Pl. I, figs. 1-12)

DIAGNOSIS. Ventri-biconvex valves of subquadrate outline; ventral valves averaging six-sevenths as long as wide and just over one-third as deep as long, evenly and fairly strongly convex in lateral and anterior profile, with curved apsacline interarea less than one-tenth of valve length. Hinge-line about four-fifths of maximum valve width. Cardinal angles obtuse, usually prominent. Dorsal valve flatly convex, less than one-fifth as deep as long; lateral profile gently and evenly convex, anterior profile depressed medianly by a slight but invariably present sulcus, which produces a gently sulcate anterior commissure. Ornamentation of angular costae only, commonly numbering 15 on ventral valve, range 14-16, and range of 14-17 on dorsal valve where the median pair occupy the sulcus. Mean wavelength of costae about 0.75 mm. at 5 mm. anteromedian to the ventral umbo.

Ventral interior with short stout teeth supported by receding dental plates; muscle field about two-thirds as wide as long and almost two-fifths as long as valve; submedian diductor lobes extending beyond adductor scars, the latter situated on a

variably developed thickening which increases towards the front of the scar, often becoming prominent anterior to the scar where it forms a low ridge extending to about mid-valve.

Dorsal interior with sockets bounded by short blade-like brachiophores, supported posteriorly by secondary shell substance. Cardinal process passing into notothyrial platform anteriorly; posteriorly it rises steadily from the platform partially to fill and project from the notothyrium. The process always becomes narrower posteriorly, but may vary in width from very slender to broad in different specimens. Ventral surface of process smooth, diductor muscles being attached posteriorly to its dorso-lateral surfaces on either side of median eminence. Anterior to notothyrial platform the poorly defined subquadrate adductor field is divided longitudinally by low median ridge.

		Maximum length	Width
HOLOTYPE.	Ventral valve (BB.30150)	7.5 mm.	8.3 mm.
PARATYPES.	Ventral valve (BB.30151)	6.2 mm.	7.0 mm.
	Complete shell (BB.30152)	7.8 mm.	10.2 mm.
	Incomplete dorsal valve (BB.30153)	6.0 mm.	c. 7 mm.
	Dorsal fragment (BB.30154)	5.7 mm.	—
	Incomplete ventral valve (BB.30155)	7.9 mm.	c. 8 mm.
	Ventral fragment (BB.30156)	—	c. 9 mm.

DISCUSSION. The Portrane specimens of *Orthambonites* show their closest morphological similarity to two forms, *O. playfairi* and *O. lyckholmiensis*. A new species recently erected by Williams (1963: 350) from the Gelli-grin Group at Bala, *O. cessata*, is also similar in the style of its ornamentation, having about 15 subangular costae, which compares closely with the distribution of 14–16 costae on 3, 13, 5 Portrane ventral valves. The wavelength of the ribs, measured medianly at 5 mm. anterior to the umbo, in three specimens of *O. cessata* is 0.5, 0.5 and 0.7 mm.; the figures for 10 Portrane valves are 0.6, 0.6, 0.65, 0.7, 0.75, 0.75, 0.85, 0.9, 0.9, 0.9 mm. A Rank Sum Test indicates that the ribs of the Welsh form are significantly narrower than those of the Irish one, $P = 0.038$. While there is no significant difference in the relative thickness of the ventral valves of the two forms, three Bala dorsal valves have ratios of 23, 24, 25% for the thickness: length of the dorsal valves, compared with 15 and 17% for two Portrane valves. The Portrane dorsal valves, then, are shallower and also possess a clearly marked dorsal sulcus, which is obscure in *O. cessata*. The high interarea of *O. cessata* further separates the two forms.

Reed (1917: 829) erected the species *O. playfairi* for specimens from several horizons in the Girvan area. Recently Williams (1962: 97) has re-described this form, and in so doing has restricted *O. playfairi* to the forms from Craighead. The Scottish shells have a similar number of ribs to the Portrane shells; their wavelength, taken 5 mm. anteromedianly to the dorsal umbo, is 0.87 mm. (var. 0.004) in a sample of 14 valves, which shows no significant difference from the 0.81 mm. (var. 0.092) recorded for 5 Portrane valves.

Williams (1962: 97) states that the ventral valve of *O. playfairi* is "less than one third as deep as long", his sample of 33 specimens having a mean of 31.8% (var.

18.0) for this character. A sample of 10 Portrane valves has a mean of 36.2% (var. 19.06) ; on testing, the latter proves to be significantly deeper ($.01 > P > .001$). Although the outline of the average Portrane ventral valve tends to be more transverse than the Craighead shells, tests comparing the a's and b's show that the difference is not significant.

The length of the ventral muscle field : length of ventral valve is given as less than two-fifths for *O. playfairi* ; 37 and 39% for two Portrane valves compare closely with this figure. Due to the faint nature of the impressions, no data are available on the dimensions of the dorsal muscle field of the Portrane species.

From Williams' original data the width of the interarea : maximum valve width was calculated for 4 valves, the figures being 60, 62, 71, 79%. The figures for this character in 7 Portrane valves are 75, 76, 78, 78, 80, 80, 85% and a comparison by Rank Sum Test shows the Portrane shells to have a significantly wider hinge-line ($P = 0.036$).

A further difference between the two forms appears to exist in the relative lengths of the ventral interareas, which are very short in the Portrane specimens. In 5 of these valves, the length of the interarea : valve length is 7.5, 7.6, 8.7, 9.3, 9.5%, with a mean of 8.5% (var. 0.86). Unfortunately, Williams does not include data for this feature, but his figured specimen (pl. 7, fig. 41) at least has a better developed interarea than any of the Irish specimens, the length being over 10% of the valve length.

Reed figured three specimens from the Whitehouse Beds (1917 : pl. 5, figs. 30-32) ; in his description (p. 831) he stated that these are especially comparable to *O. lyckholmiensis*. Apart from Reed's fig. 31 of a ventral valve, which has a hinge-line somewhat wider than those of the Portrane sample and also 17 costae, the other characters that can be ascertained from these three figures are not inconsistent with the data for the Portrane valves, and on the relative lengths of the hinge lines are certainly closer to the Portrane valves than to the *O. playfairi* from Craighead. It will, however, be necessary to obtain a sample of the Whitehouse specimens in order to clarify their exact relationships with the Portrane valves.

O. lyckholmiensis was erected by Wysogorski (1900 : 231) for forms from the "Lyckholm Stratum" of Estonia ; according to Jaanusson (1944 : 96), the well known and richly fossiliferous Lyckholm *sensu stricto* occurs in the Lower (Kõrgessare) zone of the Vormsi (F_{1b}) stage.

From Wysogorski's figure (pl. 8) it may be noted that the dorsal valve is about a quarter, and the ventral about a third, as deep as long. The Estonian forms have recently been re-described by Oraspöld (1959 : 57), who describes the ventral valves as being moderately convex, and the dorsal valves as weakly convex with a flat sulcus. His table of dimensions (p. 58) only gives the thickness of complete shells, but his lateral view of a shell (pl. 2, fig. 2a) shows the dorsal valve to be about 30%, and the ventral valve to be about 36%, of their respective lengths. This confirms the evidence of Wysogorski's figure ; thus, whilst the depth of the ventral valves of the Estonian and Portrane shells is very similar, the former possess much deeper dorsal valves.

A comparison of the length : width ratios obtained from Oraspöld's table with those of the Portrane valves shows no significant difference ; in the ribbing, outline, hinge-length and ventral interior the two forms are also closely comparable. In the dorsal interior, although there is a tendency for the rather blade-like brachiophores to become thickened in the Portrane shells as in the Estonian forms, differences can be seen in the cardinal process. Oraspöld described that of *O. lyckholmiensis* as being " thick, and in the posterior part, wedge-shaped ". His figure (pl. 2, fig. 4) confirms this. Although some of the cardinal processes of the Portrane shells are quite broad, the majority are slender ; but even the broad ones show a posterior tapering to the process, in contrast to those of the Estonian valves.

Wiman (1907 : 8) ascribed specimens from the Leptaena Limestones of Dalarne, Sweden, to Wysogorski's species ; his figures (pl. 2, figs. 9-12) show a much closer resemblance to the Portrane valves than to the Estonian form ; for, apart from having characters common to both, the thickness of the dorsal valve (fig. 10) is comparable to that of *O. humilidorsatus* (being about 18% of the valve length) ; the cardinal process is slender and, more important, tapers posteriorly ; the brachiophores are slender ; the delthyrium is wide and the interarea very short ; all these features indicate the closer affinity of Wiman's shells to those from Portrane rather than the Estonian forms.

In conclusion, the new species is very close to the Estonian *O. lyckholmiensis*, but may be distinguished from that species by the much shallower dorsal valve and the features of the dorsal cardinalia. The species identified by Wiman from the Leptaena Limestone appears to be conspecific with *O. humilidorsatus* ; whilst the forms from the Girvan Whitehouse Beds attributed to *O. playfairi* by Reed may also belong to this species.

Genus **TAPHRORTHIS** Cooper 1956

***Taphrorthis* ? sp.**

(Pl. 1, figs. 13-20)

DESCRIPTION. Shallowly biconvex valves of transversely subquadrate outline ; growth lines on a dorsal valve show the length to be just over half of the width in very early growth stages, this ratio increasing with increased growth of the valve. Posterolateral margins straight, narrowing or widening anteriorly, so that the width of the hinge-line is variable, but usually about equivalent to the maximum valve width. Dorsal valve between one-sixth and one-eighth as deep as long ; lateral profile gently convex with maximum convexity umbonally ; anterior profile depressed medianly by a variably developed sulcus which dies out anteriorly. Interarea flat, anacline, about one-ninth of the valve length ; notothyrium open. Ventral valve somewhat deeper, with greatest depth umbonally ; short apsacline interarea, delthyrium modified by lateral plates ; no fold corresponding to the dorsal sulcus, although the median rib is prominent posteriorly. Ornamentation of well-defined concentric fila (about 4 per mm.) imposed on radial costae and costellae ; about 26 ribs developed at the beak, only a few of which appear to be secondary, having arisen from costae within a mm. of the apex ; only sporadic costellae produced

until between 7 and 10 mm., when a generation appear, with a further generation developed later.

Ventral interior with teeth supported by receding dental plates ; broad, rather short, bilobed muscle field, with diductors extending beyond and not enclosing the adductor scars. Dorsal interior with simple ridge-like cardinal process on a variably thickened notothyrial platform which extends anteriorly to about mid-valve as a low ridge ; brachiophores short, slender and pointed distally, with bases convergent on to the notothyrial platform.

Material	Length	Width
Dorsal fragment (BB.30157) . . .	14.2 mm.	—
Dorsal valve (BB.30158) . . .	14.6 mm.	c. 18 mm.
Ventral fragments BB. 30159-61 . .		

DISCUSSION. The fragmentary nature of the small quantity of material available is reflected in the shortage of data. The numbers of ribs at 2 and 3 mm. from the dorsal umbo in two valves are 26 in each case ; a third shows 13 and 16 at these respective distances developed on half the valve. Half-valve measurements at 5 and 10 mm. for two valves are 18, 19 and 28, 31 at the respective distances. At 5 mm. from the dorsal umbo, 2 valves showed 4 ribs per 2 mm.

The closest of the other Portrane shells to this species is *Dolerorthis inaequicostata* (p. 190), but the species provisionally assigned to *Taphrorthis* may be clearly distinguished by the large number of ribs developed at the umbo, the less regular pattern of costellae development, the flatter valves and impersistent nature of the dorsal sulcus, and by the dorsal cardinalia where the brachiophores are quite different from the blade-like ones of *Dolerorthis* which are further grooved on the inside surface and have rounded extremities.

The shells show a strong resemblance to *Taphrorthis*, and conform to Cooper's description of that genus (1956 : 326) in all features except the five generations of costellae, the linear nature of the ventral diductor scars and the median ridge dividing the adductor field which extends "as far as the middle" (of the valve). The type species, *T. emarginata*, possesses a sulcus in the dorsal valve which persists to the anterior margin ; but in Cooper's other species, *T. peculiaris*, the sulcus becomes obsolete at the front of the shell as in the Portrane form.

Of the costae developed at the beak, a few branch very close to the beak ; these costellae would correspond to Cooper's second generation. Prior to the main costellae development that takes place between 7 and 10 mm., only a few sporadic costellae develop ; these may correspond to Cooper's third generation, although one hesitates to apply that term to such a sparse development. The main costellae development may certainly be termed a generation ; rather less prolific is a later generation, which was observed on only one valve.

The ventral diductor scars seen in the Portrane fragments could hardly be termed "linear", but this would seem to be a rather variable character in the genus (cf. Williams 1962 : pl. 8, fig. 34). A more important difference is the absence of the ridge which divides the ventral adductor scar and extends to the middle of the valve in *Taphrorthis*. This ridge is not apparent in Cooper's figure of *T. peculiaris* (1956,

pl. 38, fig. 18), although it is certainly present in the Scottish stocks described by Williams, sometimes approaching *Glossorthis* in the development of a pseudospondylium (1962 : 104).

In view of the absence of this ridge in the Portrane ventral valve, and the small and fragmentary nature of the sample, the forms are here placed provisionally as *Taphrorthis* ? sp.

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper 1931

Genus **NICOLELLA** Reed 1917

Nicolella actoniae (J. de C. Sowerby)

(Pl. 2, figs. 1-7, 10, 11)

1839 *Orthis actoniae* J. de C. Sowerby in Murchison : 639, pl. 20, fig. 16.

1846 *Orthis actoniae* Sowerby ; M'Coy : 28.

1853 *Orthis actoniae* Sowerby ; Medlicott : 268.

DESCRIPTION. Plano- to gently concavoconvex valves of subquadrate outline ; cardinal extremities acute, mucronate. Ventral valves strongly convex, about one-third as deep as long and four-fifths as long as wide, with the transverse, deep shells of young adults becoming elongate and relatively less deep with increased size. Maximum width normally at the hinge-line, but in older shells the width at mid-valve occasionally becomes slightly greater. Interarea short, curved orthocline to anacline ; delthyrium open. Protegulum of dorsal valve convex, the valve quickly becoming gently concave, with length averaging two-thirds of the valve width ; interarea short, flat, slightly hypercline ; notothyrium filled by cardinal process and chilidial plates. Concentric ornament of sporadically developed lamellose growth lines ; radial ornament of 10 to 12 angular initial costae (most commonly 10) on the dorsal valve, with additional costae appearing along the hinge-line to produce between 11 and 16 (most commonly 12) by the 7.5 mm. growth stage ; about half the sample develop costellae (internal) by this stage, with 4a usually appearing first. Wavelength of ribs just over one mm. at the 5 mm. growth stage.

Ventral interior with teeth supported by short dental lamellae ; pedicle callist well developed, otherwise muscle field and pallial markings poorly preserved. Dorsal interior with high simple cardinal process flanked by chilidial plates ; brachio-phores widely divergent, the distance between their distal extremities being about one-quarter of the valve width ; notothyrial platform continued anteriorly as a low median ridge reaching the front of the subquadrate adductor scars.

Figured Specimens	Length	Width
Complete shell, slightly broken anteriorly (BB.30162)	—	c. 20 mm.
Ventral valve, broken anteriorly (BB.30163)	—	c. 20 mm.
Deformed dorsal valve (BB.30164)	—	c. 23 mm.
Broken dorsal valve (BB.30165)	—	—
Ventral fragment (BB.30166)	—	—

DISCUSSION. In order to swell the statistical data, the amount of which was not very large due to the partly broken nature of the larger shells in particular, use has been made of well-marked growth stages, for these do register the true shape of the valve during development (Wright, 1960 : 260).

A re-description of *Nicolella actoniæ* has recently been given by Williams (1963 : 352), based on material obtained from the Actonian Stage of the Caradocian at Acton Scott, Shropshire. In the same paper he erected a new subspecies, *N. actoniæ obesa*, for the earlier form from the Gelli-grin Beds at Bala. This differs from *N. actoniæ* in its smaller size and in possessing relatively deeper ventral valves.

A consideration of the depth of the ventral valves indicates that the growth of the Portrane shells is allometric, a feature not evident in either of Williams' samples ; the data for the Portrane shells, with full data for Williams' samples, are given in Table 1. A comparison of the Portrane material with the Bala and Acton Scott samples shows that it is not distinguishable from either, there being no significant difference in the values of α or β . The Portrane ventral valves vary in length from about 2 mm. to almost 26 mm.; so that in absolute size they are closer to the Acton Scott form, rather than the Bala form.

The following data were obtained for the length (l) : width (w) of a sample of 9 dorsal valves from Portrane : \bar{l} (var. l) = 8.85 mm. (10.21) ; \bar{w} (var. w) = 13.15 mm. (21.96) ; $r = 0.9638$; a (var. a) = 1.467 (0.02185) ; $\log_e l$ (var. $\log_e l$) = 2.1191 (0.1226) ; $\log_e w$ (var. $\log_e w$) = 2.5167 (0.1193) ; $r_e = 0.9661$; α (var. α) = 0.9863 (0.000986). Tests for allometry proved negative, but allometric data are included above in order to make comparisons with the figures given by Williams (1963 : 355) for *N. actoniæ*, whose larger sample reveals allometric effects. The comparisons of the α 's and β 's reveal that the differences between the two forms are not significant at the 5% level.

No figures were given by Williams for the length : width of the ventral valve. A sample of 12 Portrane valves produced the following data : \bar{l} (var. l) = 10.0 mm. (50.1) ; \bar{w} (var. w) = 12.05 mm. (38.0) ; $r = 0.9317$; $\log_e l$ (var. $\log_e l$) = 2.0996 (0.4060) ; $\log_e w$ (var. $\log_e w$) = 2.3727 (0.2325) ; $r_e = 0.9462$; α (var. α) = 0.7567 (0.007553).

Data on the ventral muscle scars of the Portrane shells are sparse, due to the very light nature of the impressions. Accordingly, width : length ratios were obtained for two valves only, these figures (83%, 88%) being comparable to the mean (c. 90%) of the Acton Scott forms.

Only one specimen shows the ratio of length of scar ; valve length (32.5%). One of Williams' 12 specimens has a ratio of 31%, but the mean is much higher (c. 41%). Thus the muscle scar may be shorter relative to valve length in the Portrane shells, but no definite conclusion can be derived from the evidence of this solitary valve.

Measurements show the ratio of the width of the brachiophores to the valve width in four shells to be 19, 22, 24, 29% ; no figures were given by Williams for this character.

In the ornamentation, the wavelength of the ribs measured 5 mm. anterior to the umbo in 21 dorsal valves is 1.16 mm. (var. 0.0198) ; a "t" test shows this to be significantly larger ($0.05 > P > 0.02$) than the figure given by Williams for the Acton Scott forms (1.05 mm., var. 0.023 for 15 valves). Like these shells, the pattern of the Portrane dorsal valves consists basically of 5 costae on either side of the median plane, occupying a sector of about 125° , with other costae developed later in the posterolateral regions, so that a count at the 7.5 mm. growth stage shows 11-16 primaries on 2, 5, 0, 1, 1, 1, valves. Within this growth stage, 10 out of 21 dorsal valves developed secondary costellae branching internally from one or more costae, with 4a- usually the first to develop ; in a sample of 9 valves it arises first in 6, and second in the other 3 valves ; 1a- arises before 3a- in 3 out of 5 specimens. Thus the Portrane shells tend to have fewer costae and more costellae developed in the early stages than in the Acton Scott shells, but 2×2 contingency tests reveal that the differences in these samples, and in the sample from Bala, are not significant at the 5% level.

The only significant difference established between the Portrane sample and the Acton Scott sample is that of the rib wavelength ; but the actual difference is so small that it does not seem to justify even a subspecific difference, and so the shells are accordingly placed as *Nicolella actoniae* s.s.

The *N. actoniae* stock thus appears to have been fairly stable over a considerable period of time. In the Girvan area, it is interesting to note that Reed (1917 : 860) said that this species is only known with certainty from the Whitehouse Beds at Shalloch Mill ; the forms from the later Drummuck Beds and earlier Craighead Limestones (see Williams 1962 : 104) are quite distinct.

TABLE I

n	A. 15	B. 22	C. 15
\bar{l} mm. (var. l)	10.51 (47.8)	15.11 (20.912)	8.95 (11.804)
\bar{t} mm. (var. t)	3.81 (4.63)	4.61 (1.928)	3.71 (2.566)
\bar{r}	0.9766	0.9877	0.8433
$\log_e \bar{l}$ (var. $\log_e l$)	2.1726 (0.3596)	2.6713 (0.0881)	2.1231 (0.1371)
$\log_e \bar{t}$ (var. $\log_e t$)	1.1993 (0.2767)	1.4846 (0.0872)	1.2252 (0.1716)
\bar{r}_e	0.9817	0.9766	0.8364
α (var. α)	0.8772 (0.002735)	0.9949 (0.00225)	1.119 (0.0290)

TABLE I. Statistics of length (l) and maximum thickness (t) of ventral valves of *Nicolella actoniae* (J. de C. Sowerby) obtained from Portrane (A) and Acton Scott (B), and of *N. actoniae obesa* Williams from Bala (C).

Family ORTHIDIELLIDAE Ulrich & Cooper 1936

Genus *PORTRANELLA* nov.

DIAGNOSIS. Ventri-biconvex shells of sub-elliptical outline, hinge-line less than maximum valve width ; ventral valve with maximum convexity close to incurved beak. Interarea short, curved, apsacline ; delthyrium open. Dorsal valve with median sulcus ; interarea very short, anacline ; notothyrium filled by cardinal

process. Ornamentation of strong, angular costae and costellae. Shell substance impunctate?

Ventral interior with short teeth showing crural fossettes, supported by thick dental plates ; muscle field sub-oval, pedicle callist thick. Dorsal interior with short, stout brachiophores whose bases diverge ; fulcral plates absent. Shaft of cardinal process obsolete ; myophore trilobed, situated posteriorly to brachiophores, with lateral lobes extending over posterior surface of brachiophores ; thickening of valve floor between brachiophores passing into low rounded ridge extending to almost mid-valve.

DISCUSSION. Although the individual structures found in *Portranella* show strong similarities to those of several impunctate and punctate stocks, the assemblage of characters is quite distinct from that of any other described brachiopod.

With regard to the shell substance, one ventral valve shows a series of dark spots on some costae when the surface is moistened ; but it seems very doubtful if these are traces of endopunctuation. No other suggestion of it was observed in the other specimens. The failure to detect punctuation is unfortunately not conclusive ; for although the punctate nature of the shell can be seen in very finely silicified material, its absence may be due either to the shell being impunctate originally or to the obliteration of the puncta during the replacement of the shell substance by the silica.

Trilobed cardinal processes are found in both the Orthacea and Dalmanellacea, although lobate processes in general are more common in the latter. Among the Orthacea, this type of cardinal process is chiefly restricted to the Orthidiellidae ; however, *Schizoramma* is potentially trilobed and is commented on here as its external ornamentation has a similar aspect to that of *Portranella*. The cardinal process of *Schizoramma* is a simple ridge, but on the notothyrial platform on either side is an accessory ridge (Schuchert & Cooper 1932 : 88, pl. 5, fig. 14) ; a posterior rotation of these structures would produce a cardinal process simulating that of *Portranella*. The reverse process of a simplification of the *Portranella* type to the *Schizoramma* type is more difficult to envisage ; but this is what would have to take place if the later (Silurian) *Schizoramma* was evolved from *Portranella*.

A consideration of the cardinalia in particular, shows that there is a much stronger case for the present placing of the genus within the Orthidiellidae, than in any other orthaceid and dalmanellaceid stock. The Orthidiellidae have so far only been recorded in the Lower Ordovician rocks of North America, although Wang (1955 : 336) erected a genus, *Eosotrematorthis*, from the Lower Ordovician of China which he considered to be close to the orthidiellid *Trematorthis*, whilst another of Wang's genera, *Lepidorthis*, was tentatively placed in the Orthidiellidae by Alichova (1960 : 186), although it is probably congeneric with *Glyptorthis* and quite remote from the orthidiellids.

The American genera *Trematorthis*, *Orthidiella* and *Orthidium* all possess triangular trilobate myophores, sometimes with accelerated growth of the median lobe (as in *Orthidiella*) to stimulate a simple cardinal process, and which was in fact regarded as such in Ulrich & Cooper's definition of the family (1938 : 107), although they described *Trematorthis* as having a trilobed cardinal process (p. 112). The important

feature of the cardinal process in the orthidiellids is that it is fused or united to the brachiophores by shell substance (Ulrich & Cooper 1936 : 621). In *Portranella* it is this fusion that, in the absence of definite evidence on the shell structure, suggests a close relation to the Orthidiellidae rather than to those dalmanellids which possess trilobed myophores, e.g. *Resserella elegantula* Dalman, and especially also the *Paucicrura* with a high median lobe as in *Orthidiella* (the *Cristiferina* of Cooper 1956 : 961, see Williams & Wright 1963 : 29) ; for in these dalmanellids the cardinal process is sharply demarcated from the brachiophores by the longitudinal grooves forming the continuation of the notothyrial margins.

From the specimens of *Orthidiella* examined by the writer, and from figured posterior views of the dorsal valve of that genus (Ulrich & Cooper 1938, pl. 17, fig. 32 ; Cooper 1956, pl. 30, fig. 29) and also of *Orthidium* (Ulrich & Cooper 1938, pl. 16, fig. 29), there appears to be no overstepping of the notothyrial margins on to the brachiophores by the lateral cardinal process lobes as in *Portranella*. A tendency for this to occur is, however, seen in *Trematorthis masoni* (see Cooper 1956, pl. 29, fig. 12).

This strong lateral growth of the cardinal process over the brachiophores is a distinctive character in *Portranella* ; the genus may be further differentiated from the other Orthidiellidae by its much coarser, angular ribbing, its shorter hinge and more oval outline ; from *Orthidiella* and *Trematorthis* by the open delthyrium ; and from *Orthidium* by the lack of imbricate ornamentation.

TYPE SPECIES. *Portranella angulocostellata* sp. nov.

***Portranella angulocostellata* gen. et sp. nov.**

(Pl. 2, figs. 12, 13, 15-19, 21, 22)

DIAGNOSIS. Sub-rounded to transversely elliptical ventri-biconvex shells ; length to width of ventral valves ranging from about 70% to 90%, dorsal valve relatively shorter ; hinge-line about two-thirds width of valve. Ventral valve about one-third as deep as long, with short, curved apsacline interarea between one-seventh and one-ninth of valve length. Lateral profile shows maximum convexity near beak, which is moderately incurved ; anterior profile convex, slightly arched medianly. Dorsal valve shallowly convex with median sulcus, deep posteriorly, shallowing towards anterior margin. Interarea very short, anacline, with cardinal process projecting out of notothyrium. Concentric ornamentation normally subdued ; radial ornament of strong angular costae and costellae. Dorsal valve typically with 12 primary costae, median pair usually arising slightly late ; by the 3 mm. growth stage generally 4 ribs in the sulcus and 6 or 7 on each flank. Branching takes place early in sector 4, normally with $4a^{\circ}4a^{-}$, and $4a^{-}3a^{-}$; density of ribs 3 or 4 per 2 mm. medianly at the 5 mm. growth stage.

Ventral interior with short teeth exhibiting variably, but usually well-developed, crural fossettes, and stout dental lamellae ; these do not, however, continue anteriorly as ridges on floor of valve, thus the sub-oval muscle field is poorly defined. Well defined pedicle callist situated apically ; a low ridge is seen to extend anteriorly from front of muscle scar in a single specimen.

Dorsal interior with short stout brachiophores whose bases diverge to bound the sockets ; valve floor between brachiophores thickened and rising posteriorly to myophore ; traces of a median longitudinal ridge (shaft) on this thickening in some specimens. Myophore trilobed, situated perpendicular to plane of valves and posterior to brachiophores ; lateral lobes extend over posterior surface of brachiophores ; median lobe may or may not be stronger than lateral lobes, and may be grooved medianly. Low rounded median ridge rising anterior to cardinalia and extending to about mid-valve.

			Length	Width
HOLOTYPE.	Dorsal valve (BB.30167)	.	6.4 mm.	9.9 mm.
PARATYPES.	Ventral valve (BB.30168)	.	5.8 mm.	c. 8 mm.
	Ventral valve (BB.30169)	.	6.7 mm.	—
	Broken dorsal valve (BB.30170)	.	—	11.2 mm.
	Damaged dorsal valve (BB.30171)	.	10.3 mm.	c. 12 mm.

DISCUSSION. The angular ribs of this species are coarse (3, 4 ribs per 2 mm. at the 5 mm. growth stage being recorded in 3, 3 valves respectively) and in pattern show similarities to *Schizoramma* or a very coarsely ornamented dalmanellid such as *Dalmanella unguis* (J. de C. Sowerby). Unfortunately, most of the dorsal valves available for rib counts are abraded umbonally, so that the naming of the ribs in the style of Bancroft (Bancroft 1928 ; 1945 : 186 ; Williams 1949 : 163) is rather hazardous. In four shells where the rib origins could be determined with certainty the following relations for the principal costellae are obtained :

Relation	Frequency
4a ^o) 4a ⁻	4/4
4a ⁻) 3a ⁻	3/3 (1)

One large dorsal valve shows a fascicle of six ribs in sector 2, four of which are internal and one external ; this appears to be exceptional.

The following rather meagre statistical data are included for comparison with other species.

1. Rib counts. (a) in the dorsal sulcus at the 3 mm. growth stage :— 2, 4, 4, 4, 4, 4, 5 ; and at the 5 mm. growth stage :— 4, 5, 5, 6, 6.
(b) on the flanks at the 3 mm. stage :— 6, 6, 6, 7, 7, 7, 7, 8 ; and at 5 mm. :— 6, 7, 8, 9, 9.
(c) Total ribs on the ventral valve at 3 mm. from the umbo in three valves is 16, 17, 18 ; and 17, 18, 20 at 5 mm. distance.
2. Thickness of the ventral valve in three specimens is 32, 33 and 39% of the valve length.
3. Length of the dorsal valve in three specimens is 64, 66 and 75% of the valve width.

Family **HESPERORTHIDAE** Schuchert & Cooper 1931Subfamily **HESPERORTHINAE** Schuchert & Cooper 1931Genus **HESPERORTHIS** Schuchert & Cooper 1931*Hesperorthis* sp.

(Pl. 2, figs. 8, 9, 14, 20)

DESCRIPTION. Large plano-convex shells with length and width of ventral valve about equal ; cardinal angles slightly obtuse, posterolateral margins gently rounded, anterolateral and anterior margins fairly strongly rounded. Ventral valve strongly convex, about one-third as deep as long, with greatest depth at mid-valve or slightly posterior to it. Interarea curved, moderately apsacline, between one-quarter and one-third as long as the valve. Dorsal valve flat, with a concavity in neanic stages ; interarea flat, anacline, about one-sixth as long as the valve. Ornamentation of rounded costae, 19, 22 and 27 being recorded for three ventral valves ; interspaces also rounded, with strong lamellose concentric growth lines, 5 per mm., well displayed. Dorsal interior with long, blade-like brachiophores, grooved on the inside and unsupported except by the notothyrial platform ; cardinal process simple. A low rounded ridge extends anteriorly from the notothyrial platform.

Figured Specimens	Length	Width
Ventral valve (BB.30172) . . .	21.2 mm.	—
Dorsal valve (BB.30173) . . .	15.4 mm.	23.9 mm.

DISCUSSION. Four complete valves and several fragments of a *Hesperorthis* are here included as *Hesperorthis* sp. In the case of the ventral valves, the features of the interior and delthyrium are obliterated, whilst the dorsal valves show the features of the interior fairly well, but are caked with silica externally. However, these shells show the typical features of the genus in the cardinalia and flat nature of the dorsal valve, and in the deep ventral valve with its long interarea and costate ornamentation.

The ribbing of the figured ventral valve is of the same density as *Plectorthis* sp. (p. 197), but this form has flat, not curved, rib interspaces, a shorter hinge-line and a more oval commissural outline.

In its sub-equal ventral length, width and ornamentation the Portrane *Hesperorthis* resembles the Silurian *H. davidsoni* (Verneuil) figured by Schuchert & Cooper (1932, pl. 4, fig. 23) ; unfortunately the evidence of the Portrane valves is insufficient for close specific comparisons to be made with other forms. It may indeed be that the specimen with 27 ribs, whose maximum depth is also posterior to that of the other two shells, is a different species or subspecies, but the significance of this sort of variation cannot be judged with confidence from the material available.

Cooper (1956 : 141) remarked that *Hesperorthis* is rare in European faunas. This is certainly true, for the more recent fossil lists show it to be absent from the Caradocian of the Bala district (Williams 1963 : 335), South Shropshire (Dean 1958 :

218) and Cross Fell (Dean 1959 : 208), and from the Lower Ashgillian at Cautley (King & Williams 1948 : 210).

Of the Girvan fauna described by Reed (1917 : 827), only his subspecies *Orthis calligramma craigensis* is referable to this genus. Williams (1962 : 107) has recorded a new subspecies from the *confinis* Flags, but Lamont's lists (1935 : 299) for the Drummuck Beds show nothing which might be referable to *Hesperorthis*. Neither do those of King (1932 : 104) for the Horton Limestone, nor of Whittington (1938a : 451) for the Ashgillian of Llansantffraid.

For other areas of Upper Ordovician rocks there are records of the species *Orthis calligramma*, for example from the Kildare and Keisley Limestones (Reynolds & Gardiner 1896 : 593, Reed 1897a : 68). This species is, however, something of a form species, and some of the specimens ascribed to it may prove to belong to *Hesperorthis*. Those included in this species from Portrane by Baily (1861 : 11) include a plectorthid and two other "orthid" fragments, but which are certainly not conspecific with *O. calligramma* as figured by Dalman (1828, pl. 2, fig. 3 a-d).

Subfamily **GLYPTORTHINAE** Schuchert & Cooper 1931

Genus **GLYPTORTHIS** Foerste 1914

Glyptorthis maritima sp. nov.

(Pl. I, figs. 21-29)

DIAGNOSIS. Subelliptical to subquadrate ventri-biconvex *Glyptorthis*. Ventral valve about five-sixths as long as wide, and about one-third as deep as long ; maximum shell width anterior to hinge-line, cardinal angles somewhat greater than 90°. Lateral profile gently convex, convexity increasing anteriorly in older shells ; anterior profile evenly convex to sub-carinate. Interarea gently curved, apsacline, about one-fifth as long as wide and one-fifth as long as ventral valve. Young stages with fold formed by high median rib (branching to produce a fascicle of 3 or sometimes 5 ribs) which becomes lost in adult life when it is replaced by a shallow sulcus, often barely perceptible except at the anterior commissure. Dorsal valve with sulcus originating at the umbo, mean width in a sample of 23 valves being 2.84 mm. (var. 0.136) at the 5 mm. growth stage ; at between 3-8 mm. (mode 6 mm.) from the umbo this flattens out and is replaced by a low, gentle fold producing a gently plicate anterior commissure. Ornamentation of costae and costellae, with freely developed secondary internal costellae on dorsal valve, 2ā arising rather late ; external 4a° and tertiaries 3a-1°, 4a-1° moderately common. Total ribs at 3 mm. ranging from 12-22 (mode 14), and at 5 mm. 17-29 (mode 21). Concentric lamellae well developed, varying from 1 to 3, but most commonly 2, per mm. at the 5 mm. growth stage, together with finer growth lines 0.1 mm. apart.

Ventral interior with subrectangular muscle scar about one-third of valve length and about four-fifths as wide as long ; adductor scar between one-third and one-half as wide as the complete scar ; anterior margin generally convex to the front, usually indented at junctions of adductor with median lobes of diductor scars on either side ; adductor scars usually extend slightly forward of diductor scars, but many terminate slightly posterior to them.

Dorsal interior with thin blade-like brachiophores, diverging at about 90° to bound the notothyrium ; notothyrial platform thick with low median ridge extending anteriorly to divide subquadrate adductor scars, whose limits are poorly defined. Cardinal process a simple, fairly strong, ridge.

	Length	Width
HOLOTYPE. Dorsal valve (BB.30174) . . .	8.7 mm.	c. 11 mm.
PARATYPES. Dorsal valve (BB.30175) . . .	10.4 mm.	c. 14 mm.
Ventral valve (BB.30176) . . .	13.9 mm.	13.1 mm.
Ventral valve (BB.30177) . . .	10.0 mm.	12.1 mm.
Damaged dorsal valve (BB.30178) . . .	—	14.6 mm.
Ventral fragment (BB.30179) . . .	12.7 mm.	—
Dorsal fragment (BB.30180) . . .	—	—
Young dorsal valve (BB.30181) . . .	c. 3.5 mm.	5.9 mm.

DISCUSSION. In view of the common occurrence of M'Coy's species *Glyptorthis crispa* in faunal lists of the British Middle and Upper Ordovician strata, a brief review of that species seems necessary, although the forms that have been figured and described under that name are all quite distinct from the Portrane shells.

M'Coy (1846 : 29) recorded his species *Orthis crispa* as occurring rarely in the Bardahessiagh Beds, Pomeroy, of Caradocian age (Harper 1948 : 50) ; occurring commonly from Tramore, where Reed (1899 : 760) also recorded the species as being common in his stage 2 of the Tramore Limestone series, of mid-Ordovician age ; and rarely in the Tirnaska Beds at Pomeroy, these beds being equivalent to the Drummuck in age (Fearnside, Elles & Smith 1907 : 116).

M'Coy's diagnosis, as observed by Reed (1917 : 843) was too brief ; but it is likely that the original description and figure would be based on the commonly occurring Tramore form rather than on the rare Pomeroy shells ascribed to the species.

Accordingly it is here proposed to restrict *Glyptorthis crispa* to the form occurring in the Tramore Limestone, and forms conspecific with it. Reed (1899 : 761) mentioned the variability of the Tramore shells and suggested that more than one species may be present ; while some features of these shells show considerable variation, other characters such as the very fine ornamentation and the dorsibiconvexity seem to be constant regardless of the actual thickness or outline of the valves in the few specimens examined by the writer. For two of these ventral valves, 41 and 45 ribs were counted at the 5 mm. growth stage ; for the Portrane material 15-24 ribs were recorded for 2, 1, 2, 4, 2, 2, 2, 0, 4, 5 specimens respectively at this growth stage, the apparent bimodality of this distribution being due to a generation of costellae sometimes being inserted relatively early.

M'Coy (1852 : 216) gave a fuller description of "*Orthis crispa*", which was based on material of Upper Bala age from the Bala district. His figured specimen (pl. 1, H, fig. 43) shows 31 ribs at the 5 mm. growth stage, apparently having an ornamentation much coarser than the Tramore shells and more like the shells from the Girvan Ashgillian Beds ascribed by Reed (1917 : 842) to *G. crispa* ; Reed's figured exterior of a dorsal valve (pl. 8, fig. 3) shows 35 ribs at the 5 mm. growth stage. The dorsal

valves of the Portrane sample show 17-29 ribs on 3, 1, 3, 3, 7, 4, 2, 3, 1, 0, 0, 1, 1 specimens respectively, higher figures than for the ventral valve, as is to be expected.

The first account of "*G. crispa*" in which the interiors are figured is that of Reed (1917, pl. 8, figs. 4-7). These Girvan shells differ from the Portrane valves in having a ventral adductor scar which is greater than half the width of the complete scar, in having a dorsi-biconvex profile, and in lacking the dorsal umbonal sulcus. They further possess a finer radial ornamentation.

Another species from the Drummuck Starfish Bed is *Glyptorthis speciosa*, only one external impression of a ventral valve being known (Reed 1944: 215). This differs from the Portrane valves in its semicircular outline with the maximum width along the hinge-line, more ribs (27 at the 5 mm. growth stage) and a much more pronounced ventral fold.

Reed's Pomeroy species, *G. transita*, based on a solitary dorsal interior (1952: 41, pl. 1, fig. 8) is inadequately described, but apparently also has its maximum width at the hinge-line and cardinal angles of less than 90°.

The Portrane shell is much closer to *G. balclatchiensis* than to any of the above forms, there being no significant difference in the outline of the valves. Williams (1962, table 11) gives data for the dorsal valves of the Scottish shells; for the Portrane sample the statistics are as follows: $n = 29$; \bar{l} (var. l) = 6.62 (5.16) mm.; \bar{w} (var. w) = 9.11 (9.70) mm.; $r = 0.9154$; a (var. a) = 1.371 (0.01129).

Both also possess an incipient dorsal sulcus persisting for about the same distance, but whilst 3/9 of these Scottish shells possess a sulcus which persists into the adult stage, the feature was lost in all of 35 Portrane valves and replaced by a fold in 25 of these.

At the 5 mm. growth stage 1-3 concentric lamellae per mm. were recorded on 8, 17, 4 Portrane dorsal valves respectively, which is significantly coarser at the 5% level than the 2-4 lamellae on 9, 15, 3 valves respectively recorded by Williams (1962: 110) for the Scottish shells.

The frequencies of the more important ribs from a sample of 34 valves, including small valves and valves which were broken or too distorted for all the ribs to be identified, are listed in order of abundance as follows:—

4a- (31), 3a- (30), 1a- (27), 5a- (21), 2a- (16), 4a° (16), 3a-1- (10), 4a-1- (10), 6a- (7). Ribs occurring less than seven times (c. 20%) not included.

TABLE 2

2a-) 4a-	0/38 (1)
2a-) 3a-	1/42
3a-) 4a-	6/20 (15)
4a°) 5a-	4/23 (2)
5a°) 5a-	1/22 (1)
2a-) 3a-1-	18/20 (1)

TABLE 2. Ribbing relationships expressed as frequencies of occurrence in dorsal valves of *Glyptorthis maritima* sp. nov. The figures in brackets indicate the frequency of specimens where the ribs arose too close together for the earlier one to be stated categorically.

The data on the rib patterns for the Portrane shells show several differences when compared with those given by Williams for *G. balclatchiensis*, although the two are similar in many respects. In the Portrane shells, $4a^{\circ}$ is of moderately common occurrence, as are the tertiary ribs $3a^{-}$ and $4a^{-}$, in contrast to *G. balclatchiensis*. A comparison of the ribbing relationships shows the most striking feature of *G. maritima* to be the very late development of $2a^{-}$ (Table 2), and a contingency test comparing the insertion of $2a^{-}$ relative to $4a^{-}$ shows it to be significantly later in the Portrane valves than in the Girvan shells ($P = .023$).

The maximum length of the ventral muscle scar relative to the valve length for 10 Portrane valves had a mean value of 33.9% (var. 16.1); a comparison with the 5 specimens of *G. balclatchiensis* whose mean is 40.2% (var. 10.25) (Williams 1962: 111) reveals a significant difference ($.01 > P > .001$). Due to the large flanking diductors in the older valves, Williams used the length of the scar along the median line instead of the maximum length as used here; as it is shown that the maximum length of the Portrane scars is significantly shorter than the median length of the Scottish shells, the difference would be even greater if comparison could have been made with the maximum length in the Scottish shells.

Summarising, significant differences are to be found between *G. maritima* and *G. balclatchiensis* in the impersistence of the dorsal sulcus, the coarser imbricate ornamentation, the greater development of ribs $4a^{\circ}$, $3a^{-}$, $4a^{-}$ and the late development of $2a^{-}$, and in the shorter ventral muscle scar of the former.

American shells of similar age may be dismissed fairly quickly as having no very close affinities to the Portrane valves; *G. pulchra* from the Maquoketa shale has a longer ventral muscle field, finer ornamentation and very pronounced and persistent dorsal sulcus (Wang 1949: 4). The type species, *G. insculpta*, also occurring in the Richmondian, again has a much finer ornamentation and a persistent dorsal sulcus (Hall 1847: 125; Foerste 1924: 110; Schuchert & Cooper 1932, pl. 6). *G. crispata* from the late Edenian-early Maysvillian Lorraine formation of New York differs in the very much shallower ventral valve and the larger number of ribs developed (Foerste 1914: 258); *G. bellarugosa*, whose type specimens come from the Trenton Decorah formation (Cooper 1956: 363), was recorded by Roy (1941: 88) from the Richmond at Silliman's Fossil Mount. Roy's solitary specimen was retained in that species by Cloud (Miller *et al* 1954: 13); the age of this fauna is however very much in dispute as the brachiopods, trilobites and ostracods generally indicate a Middle Ordovician age, whilst the cephalopods are of dominantly Upper Ordovician affinities (Miller 1954: 43). The type specimens of *G. bellarugosa* differ from the Portrane valves most obviously in the long ventral muscle scar, persistent dorsal sulcus and finer ornamentation. No species of the genus are yet known from the Upper Ordovician of Percé or of Anticosti Island.

The following statistical data were obtained for the Portrane species.

1. *Ventral Exterior.*

- (a) *Outline—length (l): width (w) of valve:* $n=14$; \bar{l} (var. l) = 7.98 (11.264) mm.; \bar{w} (var. w) = 9.49 (9.172) mm.; $r=0.9026$; $\log_e \bar{l}$ (var. $\log_e l$) = 1.9954

(0.1630) ; $\overline{\log_e w}$ (var. $\log_e w$) = 2.2018 (0.0969) ; r_e = 0.9095 ; α (var. α) = 0.7709 (0.009179).

(b) *Profile—length (l) : thickness (t) of valves* : $n=12$; \bar{l} (var. l) = 8.44 (9.412) mm. ; \bar{t} (var. t) = 2.91 (1.066) mm. ; r = 0.8156 ; a (var. a) = 0.3365 (0.003791).

(c) *Length of interarea (x) to valve length (y)*. $n=13$; \bar{x} (var. x) = 1.79 (0.2108) mm. ; \bar{y} (var. y) = 8.93 (6.211) mm. ; r = 0.8674 ; a (var. a) = 5.429 (0.6634).

(d) *Length (l) : width (w) of interarea*. $n=13$; \bar{l} (var. l) = 1.73 (0.180) mm. ; \bar{w} (var. w) = 8.20 (3.301) mm. ; r = 0.6498 ; a (var. a) = 4.282 (0.9629).

2. *Ventral muscle scar*.

(a) *Length (l) : width of muscle scar (w)*. $n=20$; \bar{l} (var. l) = 3.15 (1.140) mm. ; \bar{w} (var. w) = 2.61 (0.3694) mm. ; r = 0.8549 ; a (var. a) = 0.5693 (0.004846).

(b) *Length of muscle scar (ms) : valve length (vl)*. $n=10$; \overline{ms} (var. ms) = 2.84 (1.170) mm. ; \overline{vl} (var. vl) = 8.13 (6.836) mm. ; r = 0.9740 ; a (var. a) = 2.417 (0.03744).

(c) *Ratio of width of adductor scar : width of complete scar*. Five valves show a mean of 39.4% (var. 52.25) for this statistic.

3. The dorsal ornamentation shows a density of 2–5 ribs per 2 mm. medianly at the 5 mm. growth stage on 6, 19, 7, 4 valves respectively. The number of ribs present in the sulcus are 2, 3 for 32, 7 valves at the 3 mm. growth stage, and 2–6 on 5, 12, 10, 5, 2 valves at the 5 mm. growth stage, respectively.

***Glyptorthis maritima magna* subsp. nov.**

(Pl. 3, figs. 1–6, 18)

DIAGNOSIS. Large *Glyptorthis* of subelliptical outline ; ventri-biconvex, becoming dorsi-biconvex with increased size. Ventral valve with gently rounded sulcus developing at about the 1 cm. growth stage by the depression of an initial strong median costa at the umbo. Dorsal valve evenly convex, strongly so in larger valves with the narrow umbonal sulcus replaced by a rounded fold developing near the 1 cm. growth stage and becoming pronounced anteriorly. Concentric ornamentation of growth lamellae, 2 and 3 per mm. being recorded for two valves at the 5 mm. growth stage. Radial ornamentation of angular costae and costellae ; total ribs on ventral valves at 3 mm. growth stage varying from 12–15 and at 5 mm. growth stage 12–16 with the mode at 14 in each case.

Ventral interior with strong teeth and muscle scar similar to *G. maritima* s.s. but often showing considerable thickening marginally, especially at the front ; a pair of well defined sub-parallel *vascula media* pass anteriorly from the outer sides of adductor scar.

Dorsal interior with stout blade-like brachiophores, thick notothyrial platform with high ridge-like cardinal process. Muscle scar subquadrate, over half valve length, unequally divided into small arcuate posterior scar which bounds the curved, posterolateral part of large quadrant-shaped anterior scar. Muscle field divided longitudinally by sharp narrow ridge extending forward from notothyrial platform ;

anterior scars also divided longitudinally by low ridge which reaches a pronounced crest along anterior margin of scar. Pallial markings often well preserved.

		Length	Width
HOLOTYPE.	Dorsal valve (BB.30182) .	20.9 mm.	24.0 mm.
PARATYPES.	Incomplete ventral valve (BB.30183)	c. 19 mm.	c. 22 mm.
	Incomplete ventral valve (BB.30184)	11.6 mm.	c. 16 mm.
	Incomplete dorsal valve (BB.30185)	—	—
	Incomplete dorsal valve (BB.30186)	12.2 mm.	—

DISCUSSION. This subspecies differs from *G. maritima* s.s. in several features ; it attains a much greater size, develops a pronounced dorsal fold and ventral sulcus, has much more pronounced internal structures, and possesses a coarse radial ornamentation.

A consideration of this ornamentation is most important. One, two ribs per 2 mm. at the 5 mm. growth stage were recorded for 1, 6 dorsal valves of the larger species, compared with 2-5 ribs on 6, 19, 7, 4 valves of the smaller species in the same position. A contingency test shows the ribbing to be significantly coarser in the larger sub-species ($P < .001$).

The total numbers of ribs on the ventral valve at the 3 mm. growth stage for the large subspecies were 12-15 on 1, 2, 2, 1, specimens compared with 11-21 on 1, 0, 10, 6, 8, 2, 0, 1, 0, 0, 2 valves respectively for *G. maritima* s.s.; the two forms cannot be separated on this character. At the 5 mm. growth stage 12-16 ribs occur on 1, 1, 3, 1, 2 specimens of *G. maritima magna*, compared with 15-24 ribs on 2, 1, 2, 4, 2, 2, 0, 4, 5 specimens of *G. maritima* s.s.; this does indicate that significantly fewer ribs are present on *G. maritima magna* ($P < .001$).

Thus in *G. maritima magna* the rib pattern of early stages persists until between about 7-10 mm. before branching occurs, the ribs being consequently coarser ; so that although the ribbing of the two subspecies is comparable at the 3 mm. growth stage, the delayed branching of *G. maritima magna* produces an ornamentation of much coarser aspect.

Whilst many of the shells with the coarser ornamentation attain a length of 20 mm. or more, others are of sizes comparable to the specimens of *G. maritima* s.s. The development of a pronounced dorsal fold is a natural continuation of the trend seen in *G. maritima* s.s., but as the presence of the coarse ornamentation on smaller shells shows, these valves are not simply large specimens of *G. maritima* s.s.

The evidence would indicate that these shells probably lived in a more favourable ecological niche than those of *G. maritima* s.s., so that they grew to a larger size and at a more rapid rate, the appearance of additional costellae being dependent on a definite stage of development rather than the attainment of a particular size of the shell. Hence where a more favourable environment encouraged more rapid growth

this stage occurred after a larger quantity of shell substance had been secreted, and was thus recorded in a more anterior position on the shell surface. Accordingly these valves are designated as a separate subspecies of *Glyptorthis maritima*.

The delay in the insertion of additional costellae which produces this coarse ornamentation in the first centimetre or so of shell growth, gives the shells an aspect reminiscent of *Glyptorthis morkokiana* described from the Ashgillian beds of the Siberian Platform by Nikiforova (1961 : 93, pl. 8, figs. 1-5). This species differs from the Portrane valves particularly in having a persistent dorsal sulcus, which shows no tendency to revert into a fold.

Foerste (1924 : 110) commented on a similar retardation of insertion of some of the ribs in specimens of *G. insculpta*, which also causes some specimens to appear more coarsely ribbed than others. He regards these merely as more robust individuals : no other comparisons are made between these forms and the finer ribbed shells, but it seems probable that present day palaeontological practice may show that more than one morphological species is present in that material.

Genus **PTYCHOPLEURELLA** Schuchert & Cooper 1931

***Ptychopleurella twenhofeli* nom. nov.**

(Pl. 3, figs. 7, 8, 10-12, 19, 20, 22, 24, 28)

1914 *Orthis? lamellosa* Twenhofel : 24, pl. 1, figs. 1-3.

1928 *Orthis? lamellosa* Twenhofel ; Twenhofel : 175, pl. 15, figs. 6, 8, 9 (non fig. 7).

DESCRIPTION. Small subquadrate to subrectangular biconvex shells, thickness about three-quarters of ventral length. Ventral valve about four-fifths as long as wide, strongly pyramidal, slightly arched medianly in anterior profile, sometimes resulting in a low fold ; interarea flat, catacline, or very slightly curved apsacline, about two-fifths as long as wide, with slit-like delthyrium due to restriction by lateral plates. Dorsal valve longer than ventral in commissural length (see Text-fig. 1) with pronounced median sulcus ; interarea short, anacline, almost one-sixth as long as wide. Ornamentation of pronounced concentric lamellae, lying close to shell with density ranging from 3 to 5 per mm., most commonly 3 or 4 at the 3 mm. growth stage ; and of simple costae, typically 13 (range 11-16) on ventral valves which have a median costa with six costae on either flank ; and 12 to 14 on dorsal valves, which have a basic pattern of two costae in the sulcus and five on each flank, with the possibility of an extra rib arising on both or either flanks

FIG. 1. Diagrammatic lateral views of the ventral valves of some genera which show different values for valve length according to the direction in which the valve is measured. C = commissural length, defined as the length of the valve measured in the plane of commissure ; S = surface length, the maximum length from the umbo to the most anterior part of the valve. This latter is *usually* the maximum valve length. 1. *Schizophorella*, in which the sulcus forms a pronounced tongue ; 2. *Ptychopleurella*, with a high catacline interarea ; 3. *Vellamo*, in which the procline interarea makes C the maximum valve length ; 4. *Kullervo*, again with a high interarea producing different lengths for C and S.

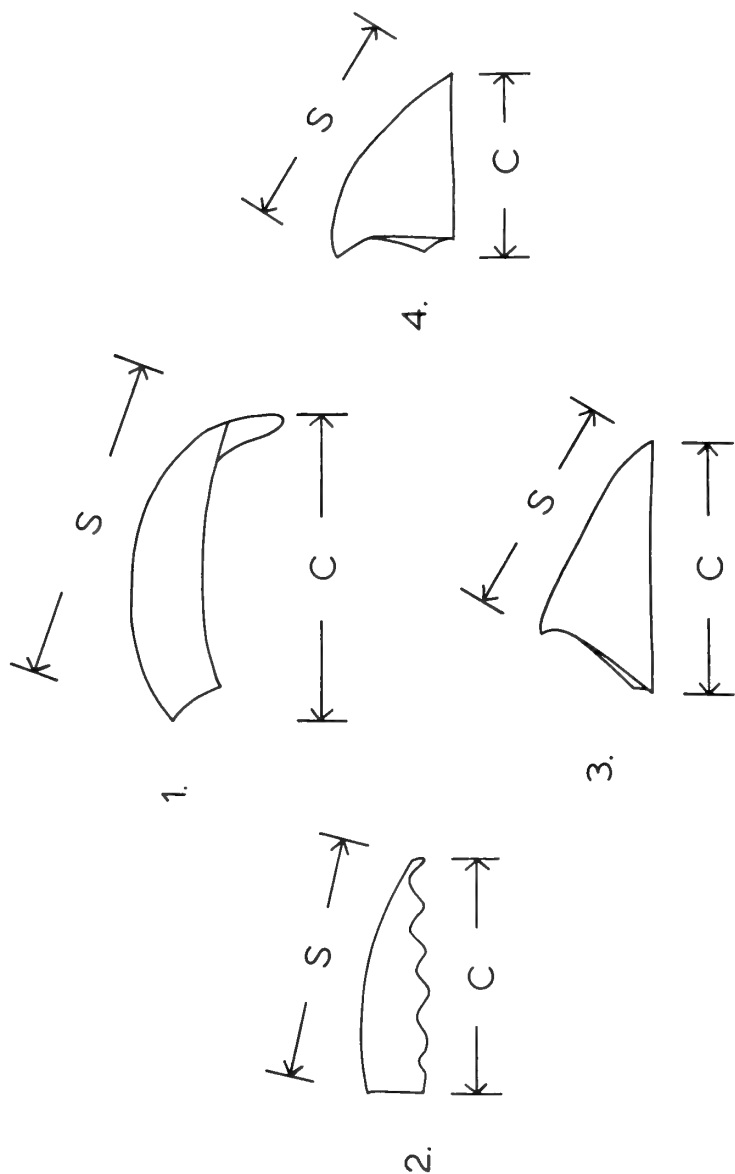


FIG. 1

between the outermost rib and the hinge-line. Extra ribs over the mode of 13 in the ventral valve developed in corresponding positions ; only one valve shows a bifurcating rib.

Ventral interior with teeth lacking support or with extremely short receding dental plates ; muscle field very small, restricted to umbonal region and of cordate to sub-triangular outline ; delicate concave apical plate present on some of the better preserved specimens. Dorsal cardinalia composed of low simple cardinal process situated on thick notothyrial platform, from which a ridge extends anteriorly corresponding in position to the external sulcus. Brachioophores short, stout, narrowly divergent ; muscle field characteristically quadripartite, but seldom preserved.

Figured Specimens		Length	Width
Complete shell (BB.30187)	. . .	5.1 mm.	4.8 mm.
Ventral valve (BB.30188)	. . .	4.5 mm.	5.1 mm.
Dorsal valve (BB.30189)	. . .	4.6 mm.	5.2 mm.

DISCUSSION. As the nature of the ornamentation of these small shells is of considerable importance in specific identification, the detailed data on the variation found in the Portrane sample are here included as follows. In the best preserved ventral valves 11 to 16 costae were recorded on 1, 0, 73, 5, 1, 1 specimens. In deformed, partially obliterated and broken valves, 13, 14 and 15 ribs were recorded for 295, 5 and 1 valves, again stressing the mode of 13 ribs. The best dorsal valves show 12, 13 and 14 ribs on 35, 20 and 30 valves ; the remaining 346 of the sample also possess the same basic pattern as stated in the description above.

Twenhofel's species *Orthis?* *lamellosa* is a member of the genus *Ptychopleurella* as defined by Schuchert & Cooper. Unfortunately, *Orthidium lamellosum* Raymond also belongs to the same genus, and has priority over Twenhofel's species which is accordingly here given a new name, *Ptychopleurella twenhofeli*. The holotype comes from the Ellis Bay Formation of Anticosti Island and is of Gamachian age (uppermost Ordovician). The following species are considered to be closest to the Portrane and Anticosti forms : *P. keisleyensis* (Reed 1897) from the Ashgillian limestone at Keisley ; *P. sublamellosa* (Cooper 1930) from the Whitehead Formation of Percé, Quebec ; *P. lapworthi* (Davidson 1883, *pars.*) from the Whitehouse Group, Girvan, and from older rocks ; and *P. uniplicata* Cooper 1956 (Benbolt Formation, Virginia).

P. rectangulata lacinata Williams from the Stinchar Limestone at Girvan also resembles the Portrane form, but may be distinguished by the significantly larger number of ribs on the Girvan shells. For the dorsal valve Williams (1962 : 112) records 11 to 18 costae inclusive as being displayed by 1, 1, 5, 16, 12, 4, 2, 2 individuals respectively. A χ^2 test shows that the number on the Portrane shells is significantly smaller ($P < .001$).

TABLE 3

	11-13 costae	14-18 costae
Stinchar frequency	7	36
Portrane frequency	55	30

TABLE 3. Table for χ^2 test comparing the ribbing densities of *P. rectangularata lacinata* from the Stinchar with *P. twenhofeli* from Portrane.

P. uniplicata Cooper possesses the number of ribs typical of the Portrane form, but has the ventral median costa raised to form a low fold. This feature does occur in the Portrane form, but here the fold is extremely variable with 1, 3 or 5 ribs raised to form a low fold, or else showing no development of a fold whatever. The outline of the ventral valve figured by Cooper (1956, pl. 49, H, figs. 43, 44) is quite different from the Portrane species in having a hinge width : valve width ratio of only 73% and cardinal angles which are very much more obtuse than those of *P. twenhofeli*, those of the latter being barely greater than a right angle.

A certain amount of confusion exists over Davidson's species *Orthis lapworthi*, which was placed in the genus *Ptychopleurella* by Schuchert & Cooper (1932 : 92). According to Reed (1917 : 843) the material figured by Davidson, and thus the type material, came from the Balclatchie Conglomerate only, and not from Shalloch Mill. Reed added that Davidson's figures and descriptions were unsatisfactory, and questioned the specific separation of *O. lapworthi* from *O. balclatchiensis* Davidson (*Glyptorthis*), the young forms of the latter being indistinguishable from *O. lapworthi*.

This last opinion was followed by Williams (1962 : 109), who included the specimens figured by Reed from the Balclatchie Conglomerate (except pl. 8, fig. 12) with the species *Glyptorthis balclatchiensis*.

The Portrane *Glyptorthis*, like the Girvan form, shows a costate condition in the umbonal region similar to that of *Ptychopleurella* ; in spite of this, and the similar development of a sulcus in the early stages, other features generally enable the two genera to be clearly separated. *Ptychopleurella* differs from young specimens of the Portrane *Glyptorthis* in showing a flat catacline or slightly curved apsacline ventral interarea whose length : width ratio is significantly larger ; and in the development of a slit-like delthyrium, resulting from its restriction by lateral plates.

Whether or not the Balclatchie specimens of *O. lapworthi* are the young of *Glyptorthis balclatchiensis*, they differ from the Portrane *Ptychopleurella* in having more costellae (ranging from 14 to 20 on the ? ventral valves—Williams 1962 : 110) although the outline and profile of the two are very similar. The shells from Shalloch Mill (Reed : pl. 8, figs. 15-17) show 12 ribs on one dorsal valve, a typical pattern for the Portrane shells, but differ in having rounded and strongly obtuse cardinal angles. The ventral valve (fig. 15) shows 14 ribs, and has no median rib judging from Reed's reconstruction of the outline. It appears more likely, however, that the specimen is deformed with the stronger median rib twisted to the left anteriorly.

The solitary ventral valve of *P. keisleyensis* possesses 16 ribs (Reed 1897a, pl. 6, fig. 1). Of the better ventral valves from Portrane, only 1 out of 81 specimens

showed as many ribs, with none amongst 301 less well preserved shells. The Keisley specimen otherwise is close to *P. twenhofeli*, although the median rib appears to be lacking, and Reed also states that there is a faint indication of a median sulcus present.

According to Cooper (1930), *P. sublamellosa* differs from the Anticosti specimens of *P. twenhofeli* in its smaller size, and in having a conspicuously larger median rib in the ventral valve. The smaller size is a questionable specific character; and the length : width ratio for the specimens whose measurements are given by Cooper (1930 : 267), i.e.

	Length	Width
Ventral valve	2 mm.	3 mm.
Ventral valve	2.5 mm.	3 mm.
Dorsal valve	3.3 mm.	3.5 mm.

clearly falls within the range of variation of that of *P. twenhofeli*, and within the actual size range of the Portrane shells. The specimen figured by Twenhofel (1928, pl. 15, fig. 9) has a width of 7 mm., whilst the widest of the Portrane specimens is 6.5 mm. Thus the Portrane shells appear almost to bridge the gap, in size at least, between the Anticosti and Percé shells. It seems doubtful whether the specimen from Battery Point (in the older Vauréal Formation) mentioned by Twenhofel (1928 : 175), which is 13 mm. wide and has 18 "small plications", does belong to the same species; unfortunately this is not figured. The conspicuously larger median rib on *P. sublamellosa* may be accounted for by the fact that in young shells, the slightly later appearance of its two bounding costae relative to the median costa and the other costae gives this appearance, the difference becoming less noticeable with increased growth of the valves. This situation is in fact to be observed in *P. twenhofeli* (Twenhofel 1928, pl. 15, fig. 8). *P. sublamellosa* shows a convex anterior margin in contrast to the straight or very gently convex margin in typical *P. twenhofeli*; but the growth lines of the latter show that in young stages it too had a convex margin, the straightening being a reflection of the development of fold and sulcus.

There seems no doubt that the Portrane shells are conspecific with the Ellis Bay shells; and on the available evidence (and in the absence of a good sample) it appears that *P. sublamellosa* is also conspecific with *P. twenhofeli*. Closely related to *P. twenhofeli* are the two British species *P. keisleyensis* and the Whitehouse specimens of "*P. lapworthi*".

The following statistical data were obtained for the various attributes of shell shape.

- (a) *Length (l) : width (w) of ventral valve.* $n=76$; \bar{l} (var. l) = 3.67 (0.705) mm.; $\log_e \bar{l}$ (var. $\log_e l$) = 1.275 (0.0507); \bar{w} (var. w) = 4.57 (0.66) mm.; $\log_e \bar{w}$ (var. $\log_e w$) = 1.504 (0.0315); $r=0.8539$; $r_e=0.8609$; α (var. α) = 0.788 (0.00217).

- (b) *Length (l) : width (w) of dorsal valve.* $n=64$; \bar{l} (var. l) = 3.75 (0.731) mm. ; $\overline{\log_e l}$ (var. $\log_e l$) = 1.296 (0.0507) ; \bar{w} (var. w) = 4.49 (0.642) mm. ; $\overline{\log_e w}$ (var. $\log_e w$) = 1.476 (0.0315) ; $r=0.7868$; $r_e=0.8154$; α (var. α) = 0.788 (0.00336).
- (c) *Ventral length (l) : shell thickness (t).* $n=20$; \bar{l} (var. l) = 3.22 (0.596) mm. ; $\overline{\log_e l}$ (var. $\log_e l$) = 1.1412 (0.0564) ; \bar{t} (var. t) = 2.39 (0.352) mm. ; $\overline{\log_e t}$ (var. $\log_e t$) = 0.0841 (0.0602) ; $r=0.9108$; $r_e=0.9200$; a (var. a) = 0.77 (0.0056).
- (d) *Width of hinge-line (hl) ; valve width (vw).* (ventral and dorsal valves) $n=73$; \bar{hl} (var. hl) = 3.8 (0.43) mm. ; \bar{vw} (var. vw) = 4.53 (0.67) mm. ; $r=0.8706$; a (var. a) = 1.24 (0.00524).
- (e) *Length (l) : width (w) of ventral interarea.* $n=44$; \bar{l} (var. l) = 1.67 (0.141) mm. ; $\overline{\log_e l}$ (var. $\log_e l$) = 0.488 (0.050) ; \bar{w} (var. w) = 4.14 (0.443) mm. ; $\overline{\log_e w}$ (var. $\log_e w$) = 1.408 (0.0255) ; $r=0.693$; $r_e=0.662$; α (var. α) = 0.715 (0.00685).
- (f) *Length (l) : width (w) of dorsal interarea.* $n=30$; \bar{l} (var. l) = 0.52 (0.009) mm. ; \bar{w} (var. w) = 3.49 (0.329) mm. ; $r=0.414$; a (var. a) = 6.047 (1.081).

"T" tests indicate allometric effects in (a), (b) and (e). The log values are also included for (c), for although a test for allometry proved negative, this may be due to the small size of the sample.

***Ptychopleurella separata* sp. nov.**

(Pl. 3, figs. 9, 13-16)

DIAGNOSIS. *Ptychopleurella* of subrectangular to subquadrate outline, with slightly convex anterior margin ; profile ventri-biconvex. Ventral valve pyramidal, about two-fifths as deep as long, with flat, procline or slightly apsacline interarea almost a third as long as wide, its width being just less than the maximum valve width. Delthyrium restricted to narrow slit by lateral plates. Ornamentation costellate ; on ventral valve five strong costae arise at the umbo ; another arising later between hinge-line and outermost costa. Median costa branching late (after 1 mm. in 9 out of 11 shells) to produce a costella on either side ; rib 2 branches to produce an external costella ($2a^\circ$), two of the valves also showing a $3a^\circ$. Corresponding costellae on dorsal exterior are internal. Six ventral valves show 9, 10, 11 ribs on 2, 2, and 2 respectively. Density of concentric lamellae 3-5 per mm. on 2, 5, 2 valves. Typical small umbonal ventral muscle field seen in one valve only, with diductors extending slightly beyond but not enclosing adductor scars.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30190).	4.8 mm.	6.9 mm.
PARATYPE.	Dorsal valve (BB.30191).	4.3 mm.	6.5 mm.

DISCUSSION. Some dozen or so specimens of *Ptychopleurella* are separated from the associated *P. twenhofeli*, being quite distinct from that form in having a costellate ribbing pattern, and at the same time having fewer ribs developed.

The outline of the ventral valve shows considerable variation from subrectangular to subquadrate. In a small sample of 6 valves for which data was obtained, the mean length : width percentage was 75.6% (var. 117.5). In contrast, the variance of the interarea was extremely small ; for the sample of five ventral valves, the mean length : width percentage of the interarea was 29.6% (var. 3.3), and its width relative to the maximum valve width was 96% (var. 1.0).

The style of ornamentation seen in *P. separata* is uncommon in the genus, the majority of species having a costate radial ornamentation, except for the two ribs in the dorsal sulcus and those flanking the median rib in the ventral valve, which do tend to develop later than the rest. The only described species whose ornamentation resembles that of *P. separata* are the much younger *P. matapedia* Schuchert & Cooper and *P. bouchardi* Davidson. The former differs from *P. separata* in having both internal and external costellae developed on costae 2 and 3 of the ventral valve ; from the latter the Portrane form differs in many features, particularly in lacking the curved, more strongly apsacline ventral interarea ; in having a restricted slit-like delthyrium ; and in lacking the embayed anterior margin.

Genus *SPINORTHIS* nov.

DIAGNOSIS. Semi-circular to subquadrate ventri-biconvex shells ; lateral profile of ventral valve markedly convex umbonally, flattening, then developing a strong, dorsally directed geniculation. Dorsal valve gently convex, with a reflection corresponding to the geniculation of ventral valve producing a marginal concavity. Dorsal valve with median sulcus, ventral valve with less prominent fold. Ornamentation of costae and costellae, together with extravagantly developed concentric lamellae directed outwards from shell surface to produce hollow spines where radial and concentric ornaments cross. Ventral interarea apsacline, but usually procline umbonally where accordingly develops a convex surface ; delthyrium broad, open, with beak often excavated. Dorsal interarea very short, notothyrium open.

Ventral interior with moderately developed teeth supported by long dental plates, which continue anteriorly as ridges to bound the obcordate muscle field. Median adductor scar narrow, separating the longer median lobes of diductor scars. Lateral diductor lobes and adjustor scars situated on inner surface of dental lamellae. A pair of closely opposed *vascula media* extend anteriorly from median diductor lobes.

Dorsal interior with a pair of weakly developed brachiophores diverging at over 90°. Sockets shallow ; cardinal process a simple ridge situated on a variably developed notothyrial platform which extends anteriorly as a ridge to divide the quadripartite adductor field longitudinally.

DISCUSSION. The imbricate external surface, the ventral muscle field, and the general appearance of the dorsal cardinalia, all indicate that the affinities of this genus lie with the Glyptorthinae. It is, however, quite distinct from any of the previously described genera of this subfamily in the extreme development of the concentric lamellae, which become directed almost perpendicularly to the shell surface to form hollow spines along the line of the ribs. A second major character of the genus is the development of a geniculation in the ventral valve, making it very deep, and a corresponding deflection in the dorsal valve. This produces an external appearance similar to a productid brachiopod, as is also seen in the Productorthinae. Other resemblances to that subfamily are found in the weak development of the brachiophores, which are indeed little more than socket ridges ; and in the extremely short interarea of the dorsal valve. These features are considered to be produced as corollaries in the development of a productoid habit in this extreme form of glyptorthinid, rather than to indicate any very close relationship with the *Nicolella-Productorthis* line, for apart from the very definite glyptorthinid characters given above, *Spinorthis* lacks the chilidial plates of the Productorthinae and unlike that subfamily possesses a well developed ventral interarea.

TYPE SPECIES. *Spinorthis geniculata* sp. nov.

***Spinorthis geniculata* gen. et sp. nov.**

(Pl. 5, figs. 1-8, 10-12)

DIAGNOSIS. Subquadrate ventri-biconvex *Spinorthis* with ventral valve three-quarters as long as wide and almost half as deep as long, and pronounced geniculation developed at about 6 mm. from umbo. Slight median fold developed posterior to geniculation, corresponding to shallow but well-marked sulcus on dorsal valve, whose initial gently convex surface becomes reflected dorsally at a position corresponding to that of geniculation of ventral valve. Ventral interarea almost one-fifth as long as valve, overall attitude apsacline, but procline umbonally due to anterior twisting of umbo to produce a convex surface ; delthyrium broad, open, with umbo excavated by the pedicle ; dorsal interarea extremely short.

Radial ornamentation of sharply crested costae and costellae, with dominantly dichotomous branching on ventral valve and intercalation on the dorsal ; radial ornamentation of strong concentric frills situated at about every mm., with finer growth lines (about one per 0.1 mm.) occasionally seen. Stout hollow spines occur where radial and concentric ornamentations cross.

Ventral muscle field obcordate, about two-fifths as long as valve ; median adductor scar narrow, less than one-quarter of the width of that of the combined adductor and median diductor lobe scars, this latter width being about two-thirds of the length of the complete scar. Adductor scar about three-quarters of the length of diductor scars. Cardinalia composed of simple cardinal process situated on variably developed notothyrial platform ; brachiophores weak, diverging at a mean angle of 100° (var. 119°) in a sample of 9 specimens.

		Maximum Length	Width
HOLOTYPE.	Ventral valve (BB.30192) .	10.6 mm.	11.9 mm.
PARATYPES.	Dorsal valve (BB.30193) .	9.8 mm.	c. 16 mm.
	Dorsal valve (BB.30194) .	9.9 mm.	11.6 mm.
	Ventral valve (BB.30195) .	9.9 mm.	12.2 mm.
	Broken ventral valve (BB.30196) . . .	—	—
	Broken dorsal valve (BB.30197) . . .	—	—
	Dorsal fragment (BB.30198) .	—	—

DISCUSSION. The sudden increase in convexity of the ventral valve in later growth stages suggests allometric growth, a feature which is confirmed statistically (data given below). This type of development affects the valve outline (the shells losing their rather transverse appearance with increased growth) as well as the convexity, the strong convexity of the umbonal stages usually flattening before the development of the geniculation, which occurs at a mean distance of 6.35 mm. (var. 0.49) from the umbo in a sample of 16 ventral valves. Two deformed valves, which are not included in these figures, show a rather later geniculation (7.9, 8.5 mm.). The corresponding deflection of the dorsal shell occurs at a mean distance of 7.15 mm. (var. 0.56) in a sample of 10 valves.

The dorsal sulcus is shallow, gently curved, and bound by a strong costa on either side, with a mean width of 1.5 mm. (var. 0.0525) at 3 mm. from the umbo in a sample of 21 valves. Within the sulcus a late costa arises medianly usually between 2 to 3 mm. from the umbo; 0.4 ribs are developed in the sulcus of 11, 5, 0, 0, 0 valves at 2 mm.; 0, 18, 2, 0, 0 valves by 3 mm.; and 0, 2, 2, 2, 1 valves at 5 mm., respectively, the additional ribs being costellae.

The basic ribbing pattern of the dorsal valves is of three strong costae on either flank, with weaker costae sometimes developed outside these; costellae also develop, sometimes by splitting, but normally by intercalation. The total numbers of ribs (including those in the sulcus) recorded at various growth stages are as follows:—At 2 mm., 5–8 ribs occur on 1, 7, 4, 2, specimens; at 3 mm., 7–11 ribs occur on 4, 2, 3, 2, 5 specimens respectively; whilst at 5 mm. counts of 11, 12, 13, 15, 15 were taken on 5 valves. The mean wave-length of the ribs taken at a distance of 3 mm. from the umbo for a sample of 15 dorsal valves is 0.71 mm. (var. 0.03). On the geniculate part of the ventral valve the ribs are less prominent and much wider spaced, whilst some ribs are barely perceptible or missing completely from the valve surface after the geniculation.

For the concentric ornamentation, 2, 3 and 4 lamellae are present over the 2 to 4 mm. distance anterior to the ventral umbo on 5, 3 and 1 specimens respectively.

Whilst the dorsal interarea is so small as to be barely visible in many specimens, the ventral interarea has a mean length : width % of 20.5 (var. 60.8) in 7 shells, its mean length being 18.6% (var. 8.3) of that of the valve length for 5 specimens.

In carrying out a statistical assessment of the muscle scars, the measurement of the width of the scar was taken across the adductor and the median diductor lobes

on either side. The lateral diductor lobes are situated on the inner surfaces of the dental plates. Accordingly, they are in a plane of anything up to 90° to that of the median lobes, and because of this variability have been excluded from the statistical data. Seven valves show a mean width : length % for the muscle scar as thus restricted of 65.4% (var. 110.5), the mean length of the scar to the valve length being 39.8% (var. 19.8) in 6 valves. Four valves show the diductors to extend in front of the adductors by 12, 26, 30, 34% of the diductor length, whilst the width of the adductors : width of the muscle scar is 22, 22 and 26% in three valves.

Statistical data for the valve shape is as follows:—

- (1) *Length (l) : width (w) of the ventral valve*:— $n=18$; \bar{l} (var. l) = 6.52 mm. (11.12) ; \bar{w} (var. w) = 8.87 mm. (11.66) ; $r=0.862$; $\log_e l$ (var. $\log_e l$) = 1.7588 (0.2323) ; $\log_e w$ (var. $\log_e w$) = 2.1137 (0.1381) ; $r_e=0.875$; α (var. α) = 0.7709 (0.009545).
- (2) *Length (l) : thickness (t) of the ventral valve*:— $n=10$; \bar{l} (var. l) = 9.53 mm. (2.59) ; \bar{t} (var. t) = 4.29 mm. (1.40) ; $r=0.7805$; $\log_e l$ (var. $\log_e l$) = 2.2405 (0.0279) ; $\log_e t$ (var. $\log_e t$) = 1.4196 (0.0734) ; $r_e=0.789$; α (var. α) = 1.622 (0.07216).
- (3) *Length (l) : width (w) of dorsal valve*:— $n=10$; \bar{l} (var. l) = 6.73 mm. (6.99) ; \bar{w} (var. w) = 8.57 mm. (14.26) ; $r=0.8414$; a (var. a) = 1.429 (0.07446).

Family **DINORTHIDAE** Schuchert & Cooper 1931

Genus **PLAESIOMYS** Hall & Clarke 1892

Plaesiomys porcata (M'Coy)

(Pl. 4, figs. 1–12)

- 1846 *Orthis porcata* M'Coy : 32, pl. 3, fig. 14.
 1853 *Orthis porcata* M'Coy ; Medlicott : 268.
 1861 *Orthis porcata* M'Coy ; Bailly : 11 (*pars*).
 ?1870 *Orthis porcata* M'Coy ; Davidson, pl. 31, fig. 13.
 1880 *Orthis porcata* M'Coy ; Bailly : 81 (*pars*).
 1895 *Orthis porcata* M'Coy ; Sollas : 102.

DESCRIPTION. Dorsi-biconvex to convexo-concave shells of transversely elliptical outline ; ventral valves about three-quarters as long as wide and one-quarter as deep as long, maximum thickness at or close to the umbo. Cardinal angles obtuse, with the hinge-line width about four-fifths of the maximum valve width. Interarea about one-fifth as long as wide, and about one-fifth as long as the valve, flat or gently curved (especially near the beak) ; attitude varying from apsacline to catacline and procline. Delthyrium normally open ; one specimen however shows what may be a concave pedicle collar at the apex. Lateral profile variable, depending on the attitude of the interarea ; where this is apsacline, the deepest part of the valve is just anterior to the umbo, after which the valve flattens ; in procline valves the beak is usually (although not invariably) the deepest part, anterior to

which the valve is flat or slightly concave. Transverse profile low, conical. Shallow sulcus developed in the young adult stages, flat or smoothly curved producing a gently plicate anterior commissure.

Dorsal valve evenly convex in both profiles, the convexity increasing relatively with age ; thickness : length ratios ranging from one-sixth to almost one-half in a large shell (35 mm. long) ; interarea less than one-tenth of the valve length, curved, orthocline to slightly apsacline. Ornamentation of rounded to sub-angular ribs with costellae developing from about 19 primary costae, the total number of ribs having a mode of 28 (range 20-35) at the 5 mm. ventral growth stage, and a mode of about 40 (range 36-48) at the 10 mm. growth stage ; shells of this latter size usually have a maximum of three ribs per sector, whilst those attaining 20 mm. may have 5 or 6 in some sectors due to the development of additional costellae at about this size.

Ventral interior with teeth supported by strong receding dental plates whose anterior continuation forms the margin to a sub-triangular to subpentagonal muscle field, extending for about one-third of the valve length and much thickened by secondary shell substance. Pedicle callist well defined ; adductor scars small, elongatedly oval, subcentral, almost enclosed by the triangular median diductor lobes ; lateral lobes usually well-developed, with adjustor scars on the inner surface of the dental plates. Ridges of the arcuate *vascula media* arise from the antero-lateral extremities of the muscle field and branch across the valve floor.

Dorsal interior with cardinalia consisting of simple brachiophores extending anteriorly for about one-sixth of the valve length, the tops diverging at about 90° (7 specimens have a mean of 89°, variance 84.3) and are supported by shell substance only, to form the inner boundary of the sockets ; the brachiophore may have a smooth or grooved inner surface, sometimes with a ventrally directed hook at its distal end. Notothyrial platform shallow, with a high cardinal process, grooved posteriorly on its antero-ventral surface where the shaft passes into a large myophore. The platform extends anteriorly as a low ridge to divide the adductor field, whose length and width are about equal, with the subtriangular anterior scars smaller than the sub-oval posterior pair. *Vascula media* and *myaria* occasionally well defined.

Figured Specimens	Length	Width
Ventral valve (BB.30199)	24.1 mm.	35.7 mm.
Damaged ventral valve (BB.30200)	—	—
Damaged dorsal valve (BB.30201)	35.4 mm.	c. 40 mm.

Also four ventral fragments (BB.30202-05) and four dorsal fragments (BB.30206-09).

DISCUSSION. One of the most important characters of the genus, and indeed of the family Dinorthidae, is that of the ventral muscle field. In this species a sample of 13 valves show a mean length : width ratio for the muscle scars of 107% (var. 500.6), the high variance indicating large differences in the overall outline of the scars. The muscle field shows a well-developed pedicle callist umbonally, antero-median to which is a groove which broadens into an elongatedly oval adductor field. The bounding median lobes of the diductor scar practically enclose the adductor field anteriorly, except for a narrow groove which produces a median notch in

the otherwise straight anterior edge of the muscle field. The antero-lateral angles of the median diductor lobes are almost 90° , giving a squarish appearance to the front of the scar. Outside these are the lateral lobes of the diductor scars, whose convex outside margins give a rounded aspect to the whole scar when strongly developed. These are the adjustor scars of authors (Schuchert & Cooper 1932, e.g. pl. A, figs. 12, 13; Moore, Lalicker & Fischer 1952 : 208, text-figs. 6-10); the adjustor scars are however found immediately outside these on the inner surface of the dental lamellae, and there seems little doubt that the disposition of the scars is similar to that of the closely related dalmanellid stocks, rather than to that of the Recent terebratuloids (see Williams & Wright 1963 : 16).

As may be expected from the development of a sulcus, the costellae of the ventral valve are more commonly internal than external, although both do occur; where a costella arises on either side of a costa, the tendency is for the internal one to arise first.

Rib counts on the ventral valves show 16-21 primary costae on 2, 0, 2, 0, 1, 3 valves, other estimates where the ribbing was partly obliterated also falling within this range and suggesting a modal number of about 19. The wavelength of the median rib was measured at 5 and 10 mm., but the figures vary greatly according to the position of splitting of the ribs. Thus for rib density a more satisfactory picture is obtained from a count of the number of ribs per 2 mm. measured medianly at 5 mm. from the ventral umbo; the sample shows 2-5 ribs present on 1, 9, 5, 1 shells.

The total number of ribs was counted at three growth stages; at 5 mm. 20-35 ribs are present on 1, 0, 1, 0, 0, 1, 1, 1, 3, 0, 1, 1, 1, 0, 1 valves, which in spite of the large scatter in the 13 shells shows a distinct mode of about 28 ribs; at 10 mm. 36-48 ribs are present on 1, 1, 2, 0, 0, 1, 1, 1, 0, 0, 0, 0, 1 valves; at 15 mm. 45, 50, 51, 54, 57 ribs are present on 5 valves; whilst one complete fairly large shell (length 24 mm.) has 70 ribs at its margin.

A rib count taken on the dorsal valves at 7.5 mm. from the umbo shows 26, 27, 29, 30, 32, 32, 34 ribs present on 7 valves.

Statistical data on shell outline and profile are rather sparse due to the broken nature of the valves, especially the dorsal valve, the large size of this species rendering it very susceptible to damage. In a sample of 8 ventral valves, the mean valve length : width % is 72.9 (var. 138.7); four valves show the thickness : length ratio to be 22, 23, 24 and 27%.

A sample of 8 ventral valves have a mean % for the length of the interarea : valve length of 19.5% (var. 2.57); the length of the interarea relative to its width in 4 valves is 17, 17, 19, 22%; whilst 3 valves have identical figures of 81% for the ratio of the width of the interarea : maximum valve width.

The original description of *Orthis porcata* by M'Coy (1846 : 32) was based solely on material from Portrane, and his figure of a broken ventral valve (pl. 3, fig. 14) shows the typical ribbing pattern of the species. In M'Coy's later description of the species (1852 : 223), he figured specimens from the Coniston Limestone (pl. 1, H, figs. 41, 42) and cited some ten localities at which the form occurs. However, it

is quite certain that *P. porcata* does not occur at all of these localities ; it is not present for example in " the Caradoc Limestone of Horderly S.", which is presumably the Alternata Limestone.

Nevertheless it does appear to be a widespread form in the British Ashgillian rocks, for apart from actual descriptions of the species (Davidson 1870 : 251 ; Reed 1917 : 840) there are many records of its occurrence in rocks of Ashgillian and even of Llandoveryan age (Groom & Lake 1908 : 578).

In spite of the fragmentary nature of the Portrane shells, already mentioned by M'Coy (1852 : 223), it is hoped that the current re-description of this topotypic material will prove useful for comparison with specimens from other localities ; thus the validity or otherwise of the various records of the form can be established.

Family **DOLERORTHIDAE** Öpik 1934

Genus **DOLERORTHIS** Schuchert & Cooper

Dolerorthis inaequicostata sp. nov.

(Pl. 3, figs. 17, 21, 23, 25-27)

DIAGNOSIS. Subequally biconvex *Dolerorthis* of transversely subquadrate outline with rectangular to slightly obtuse cardinal angles ; margins slightly rounded postero-laterally and anteriorly, strongly rounded antero-laterally. Ventral valve about three-quarters as long as wide, thickness ranging from one-quarter to one-third of valve length ; lateral profile with maximum depth and convexity at about one-quarter of shell length, less convex anteriorly. Anterior profile usually evenly convex. Interarea curved, apsacline, with length about one-fifth of its width and of valve length ; delthyrium rather narrow. Dorsal valve about two-thirds as long as wide and over one-quarter as deep as long ; evenly convex in lateral profile ; convex in anterior profile, but divided medianly by well-developed sulcus ; interarea flat, anacline, about one-ninth as long as valve, notothyrium open. Ornamentation costellate, usually with 3 ribs per mm. at the 10 mm. growth stage, crossed by poorly preserved concentric growth lamellae with a density of about 3 per mm. at 5 mm. anterior to dorsal umbo. About 16 primary costae at dorsal umbo, with up to 3 additional costae along hinge-line on either side, ribs having a rounded crest and sub-parallel sides. 18-20 costae present at the 3 mm. growth stage ; only one generation of costellae, with four-fifths of the internal ones, but only about one-fifth of the external ones, developed by the 5 mm. growth stage. Costellae remain less pronounced than the costae. Sulcus occupied by 4 primary costae. Ventral ornamentation with a median rib which develops a costella on either side ; rib 2, sometimes rib 3 and occasionally rib 4 develop an external costella ; rib 5, usually rib 4, and sometimes ribs 3, 6, 7, develop a costella on either side ; ribs 8, 9 and sometimes 6, 7, develop only internal costellae, whilst ribs outside these remain simple costae. Ventral costellae arise somewhat later than the dorsal, thus at the 5 mm. growth stage there are seldom more than the 20 costae developed. At 10 mm., a total of 43 ribs were recorded for one valve.

Ventral interior with strong teeth and receding dental lamellae ; muscle field

cordate, about four-fifths as wide as long and about two-fifths as long as valve ; adductor scars narrow (one-fifth as wide as whole scar) situated on slight ridge, and about nine-tenths as long as diductor scars. Dorsal interior with simple cardinal process on notothyrial platform, anterior to which is a short low median ridge ; brachiophores short blades, grooved on the inside and triangular in cross section.

		Length	Width
HOLOTYPE.	Dorsal valve (BB.30210) .	9.6 mm.	13.9 mm.
PARATYPES.	Ventral valve (BB.30211) .	13.8 mm. c.	17 mm.
	Ventral valve (BB.30212) .	14.6 mm. c.	19 mm.
	Ventral valve (BB.30213) .	12.2 mm.	17.4 mm.
	Broken dorsal valve (BB.30214)	—	—

DISCUSSION. This species of *Dolerorthis* is characterized by the rather transverse outline, the subequal convexities of the valves, the presence of a well defined dorsal sulcus, and the rather late development of a single generation of costellae, which never attain the size of the costae, so that the latter tend to stand out clearly.

Although not many complete specimens of the new species are available, sufficient data has been obtained to carry out a comparison with the subspecies of *D. duftonensis* from the Gelli-grin calcareous ashes recently erected by Williams (1963 : 357). A small sample of topotypic *D. duftonensis* s.s. from Cross Fell was also examined by Williams, the differences between it and his subspecies *prolixa* being found in the nature of the brachiophores, the relatively longer dorsal valve, shorter dorsal interarea, deeper ventral valve, and shorter ventral muscle field of *D. duftonensis* s.s.

For the outline of the dorsal valve, the length of a single complete Portrane shell was 69% of the width ; although less than the mean (75%) this falls within the range for the Welsh form, which is significantly different from the figures of 74, 77, 85, 86, 90% for five Cross Fell specimens. Five Portrane ventral valves have a mean ratio of thickness : length of 28.8% (var. 17.7) ; the mean for the Welsh shells is very close to this at 28.6%. In a comparison with Williams' three valves of *D. duftonensis* (p. 358), with ratios of 37.5, 44.4 and 50%, the Portrane shells (24, 26, 29, 30, 35%) show a significant difference, $P=0.018$. The length of the dorsal interarea : length of dorsal valve for three Portrane shells is 11, 11 and 12%. For this statistic, the mean for the Welsh shells is 11.9%, and for *D. duftonensis* s.s. 10.4%, these two being significantly different from each other (Williams 1963 : 360). Whilst the Portrane valves are closer to the Welsh form, a Rank Sum Test shows that this sample is not significantly different from either. The mean ratio of the length of the ventral interarea : valve length for a sample of 7 Portrane valves is 21% (var. 8.0), no figures being given by Williams for this statistic.

The mean width : length ratio for the ventral muscle scar of 5 Portrane valves is 78.4% (var. 54.5), which is comparable with both subspecies of *D. duftonensis*. However, the length of the ventral muscle field relative to valve length is significantly larger in the Welsh form (26, 29, 31, 32, 35%) than in the English one (24, 26, 26, 27, 29%) ; a comparison of the Irish shells with Williams' Rank Sum data reveals that the muscle field of the Irish form (35, 36, 38, 39, 43%) is significantly longer than either ($P=0.008$).

This last is really a reflection of the shorter, more transverse nature of the Portrane shells which cannot be adequately brought out by the solitary complete dorsal valve (see above) ; Williams gives no data on the length : width of the ventral valve, but his two ventral paratypes show ratios of 91, 93% in contrast to ratios of only 70 and 81% for two complete Portrane valves. Approximations for four partially damaged Portrane valves also fall within this range, so while it seems fairly certain that the Portrane valves are more transverse than the other forms, the accurately measured samples are too small to confirm this mathematically. Again, the single perfect dorsal valve shows a thickness : length ratio of 27%, compared with a mean of 17% for the two sub-species of *D. duftonensis*.

Reed (1910 : 295) described the dorsal valve of *D. duftonensis*, which is shallower than the ventral, as having a " faint median longitudinal depression occasionally present ". Williams (1962 : 115), in placing some specimens from Craighead as *Dolerorthis* cf. *duftonensis*, states that these shells differ from *D. rankini* in the absence of a strong dorsal median sulcus ; and in describing *D. duftonensis proluxa* from the Bala district, he states that species to be " gently sulcate medianly but evenly convex in longitudinal and lateral profile " (1963 : 357).

The strong sulcus of the Portrane dorsal valves, which produces a pronounced saddle in the anterior profile, is a marked difference between it and the *duftonensis* stock.

The ornamentation of the two stocks differs in several ways. The costae of the Portrane shells are much more prominent than the costellae, whilst the two are of equal strength in *D. duftonensis* s.l. In the ventral valve figured by Williams (1963, pl. 2, fig. 8) the right flank shows the median costa with a costella on either side, the other costellae being 2a°, 3a°, 4a°, 5a°, 6a°, and 7a-, 9a-, 10a-; whilst a sample of eight Portrane valves (three of which have the ribs outside 6 obliterated) show costae 2, 3, 4 to have a single external costella 8/8, 4/8, 2/8 times ; both an internal and external costella on costae 3-8, 4/8, 6/8, 8/8, 4/7, 2/4, 1/4 times ; and a single internal costella on costae 6-9, 3/7, 2/4, 3/4, 3/3 times, respectively.

Thus while the inner ribs possess external and the outer ribs internal costellae in both forms, the double costellae of the intermediate sectors are missing in the Bala shell, at least in the type.

The Portrane valves have 16 or 17 primary ribs at the umbo with up to 3 additional ribs on either side, whilst the Bala type ventral valve shows 30 primaries, the difference being due in part to the large number developing laterally along the hinge-line. The Bala shell has about 24 ribs at the 3 mm. growth stage, compared with 19, 19, 19, 20 in 4 Portrane shells ; at 5 mm. it has 34 compared with 19, 20, 23 for 3 Portrane specimens, and at 10 mm. 50 ribs compared with 43 for a Portrane shell.

Thus although the total number of ribs is not very different, the method by which they arise is different. To summarise, the Portrane ventral valves (a) have fewer costae, with less along the length of the hinge ; (b) these persist for a greater valve length before branching, and as a result are strong costae ; and (c) the costae which are intermediate in position produce a costella on either side.

The earlier development of costellae is also seen in the dorsal valve of the Bala shells, where the 2 specimens measured by Williams (raw data) show that the early 3a⁻ is already developed by the 2 mm. growth stage in both valves, with 4a⁻ and 9a⁻ also developed in one of them ; this very early development is apparently typical (Williams, personal communication). On the other hand at the 3 mm. stage only one out of 7 Portrane shells had an internal rib developed ; this was a 3a⁻, although this rib is by no means as consistently early or the 2a⁻ as consistently late as in the Bala form, the data on rib development being given in Table 4.

TABLE 4

2a ⁻) 3a ⁻	3/5 (1)
3a ⁻) 4a ⁻	3/5 (2)
4a ⁻) 5a ⁻	2/3 (4)
2a ⁻) 5a ⁻	4/5 (1)
2a ⁻) 4a ⁻	3/5 (2)

TABLE 4. Frequencies of relative dorsal rib development in a small sample of *Dolerorthis inaequicostata* sp. nov., figures in parentheses indicating the frequencies where the costellae arise at an equal distance from the umbo.

The actual costellae developed have a similar distribution to those of the Bala shell ; as regards rib density, at the 10 mm. growth stage the ribs measured medianly over a 2 mm. distance for the Portrane shell were 3, 3, 3, 3, 4 in 5 valves. Williams' Bala shells showed 1 and 2 ribs per mm. on 1 and 7 valves measured in the same position ; in the case of the Portrane valves "one and a half ribs" per mm. was not very satisfactory, thus the count was taken over 2 mm. These figures suggest a rather coarser ribbing in the Portrane shells.

Thus, whilst the Portrane species shows features which are very similar to those of the *D. duftonensis* stock, more particularly to the Bala subspecies, it does differ, principally in the presence of a dorsal sulcus, the subequal convexity of the valves (which are more transverse), the relatively longer ventral muscle field, the uneven size of the costae and costellae, and other features of the ornamentation as indicated above.

D. rankini (Davidson) from the Ardwell Beds, Girvan, resembles the Portrane shell in the presence of a strong dorsal sulcus ; but differs in having a relatively longer dorsal valve, a relatively shorter ventral muscle scar [Williams (1962 : 114) records a mean of 33% of the valve length for this character in 3 valves, the raw data being 33, 33 and 34% ; this shows a significant difference ($P=0.018$) from the Portrane figures in a Rank Sum Test], and almost double the number of much finer ribs (having c. 90 in a valve 15 mm. long). As in the Derfel Limestone species, *D. tenuicostata*, recorded by Whittington & Williams (1955 : 406), costellae are produced by both early and late insertions of secondary ribs and also by tertiaries. The ribs of this last form are also considerably finer and more numerous with the first secondaries arising much earlier than in the Portrane shells, and like *D. rankini* have a less transverse outline ; they also lack the strong sulcus of the Girvan and Portrane shells.

Family **PLECTORTHIDAE** Schuchert & Le Vene 1929Subfamily **PLECTORTHINAE** Schuchert & Le Vene 1929Genus **PLECTORTHIS** Hall & Clarke 1892*Plectorthis* ? *perditosulcata* sp. nov.

(Pl. 6, figs. 2-6, 8, 9)

- 1861 *Orthis calligramma* Dalman ; Bailly : 11 (*pars*).
1880 *Orthis calligramma* Dalman ; Bailly : 82 (*pars*).
1895 *Orthis calligramma* Dalman ; Sollas : 101 (*pars*).

DIAGNOSIS. Ventri-biconvex shells of roundedly subquadrate outline, about four-fifths as long as wide, maximum width near mid-valve. Ventral valve about one-third as deep as long, maximum depth at the umbo ; lateral profile gently convex, anterior profile arched medianly, with rather flat flanks. Interarea about one-third as long as valve, with ratio of length to width approaching one-third ; curved umbonally, but flat over most of its length, varying from strongly apsacline to catacline. Delthyrium with small convex plate occasionally developed at apex. Dorsal valve flatly convex, usually less than one-sixth as deep as long ; median sulcus well developed at the umbo, broadening and becoming lost anteriorly by about 10 mm. or less, when the valve develops an evenly convex surface, but not a fold. Sulcus separated by elevated flanks from flat cardinal regions. Interarea flat, anacline, about one-seventh of valve length. Ornamentation of costae, square in section with rounded crests, separated by flat interspaces on which strong growth lines are preserved. Costellae also present, but of restricted distribution ; dorsal valve with single external secondary rib developed almost invariably in sectors 3, 4, less commonly in sectors 2, 5, and only occasionally in sector 6 ; only one tertiary (4a-1-) recorded in 13 valves. Ventral valve with median rib initially stronger than rib 2, external costellae corresponding to internal ones of dorsal valve, with internal rib also appearing rarely. In the dorsal valve, first costella arises at about 3 mm., but may appear over a range of from 1.5 to 6 mm. from the umbo ; 20-26, most commonly 24, ribs at the 3 mm. growth stage ; 23-30, most commonly 28, at the 5 mm. growth stage, with maximum of 34 recorded for any valve. Mean rib wavelength for 10 dorsal valves of 1.0 (var. 0.005) mm. at the 10 mm. growth stage.

Ventral interior with obcordate muscle field, larger diductor scars extending beyond narrow adductor scars ; width : length ratio of muscle field variable, 60, 77, and 85% recorded in three valves. Dorsal interior with sockets defined by small fulcral plates ; brachiophores blade-like, triangular in cross-section, supporting plates convergent on to a variably thickened notothyrial floor which bears simple, plate-like cardinal process. A low, rounded median ridge extends anteriorly from notothyrial platform to divide poorly delimited adductor field.

	Length	Width
HOLOTYPE. Ventral valve (BB.30215)	. 14.8 mm.	18.6 mm.
PARATYPES. Dorsal valve (BB.30216)	. c.15 mm.	c.17 mm.
Incomplete dorsal valve (BB.30217)	. . . 18.6 mm.	—
Ventral fragment (BB.30218)	. —	—
Ventral fragment (BB.30219)	. —	—
Imperfect ventral valve (BB.30220)	. . . 8.6 mm.	—

DISCUSSION. This new species is placed with some reservation in the genus *Plectorthis*, due to the fact that an occasional ventral valve possesses a small convex plate in the apex of the delthyrium (Pl. 6, figs. 5, 8), a feature at present unknown in *Plectorthis*, but which is characteristic of the plectorthid genus *Desmorthis*.

Desmorthis has only been recorded from the Upper Pogonip Formation in Nevada, and the Joins Formation in Virginia (Ulrich & Cooper 1936 : 624 ; Cooper 1956 : 447) both of Lower Llanvirn age (Twenhofel *et al.* 1954 : 260). Ulrich & Cooper (1938 : 158) also cited the simple thin cardinal process as differentiating their primitive genus from the later, more advanced *Plectorthis*, whose cardinal process possesses a myophore. The crenulated myophore of *Plectorthis* is not, however, as invariable a feature as it would appear from Schuchert & Cooper's discussion of the genus (1932 : 59), for *P. compacta* Cooper and *P. scotica* (M'Coy) possess a simple plate-like cardinal process, as does *P. ? perditosulcata*. The median thickening in the dorsal valve, and the usually well defined anterior margin of the diductor scars in the Portrane species, tend to militate against inclusion with *Desmorthis*. The exact systematic value of the "deltidium" at this stage in the evolution of the plectorthids is difficult to ascertain, but in view of the large disparity in time between these Upper Ordovician forms, and the known *Desmorthis* species, it seems better for the present to regard the Portrane shells as being closer to *Plectorthis*, with the occasional occurrence of a "deltidium" most probably representing a late morphological convergence towards an ancestral stock. Unfortunately most of the material is fragmentary, with many broken delthyria and others which are caked with silica (as in the holotype), so that the frequency of occurrence of the feature cannot be established with accuracy.

Of the two described species of *Desmorthis*, the Portrane shell more closely resembles *D. costata* Cooper, which, although it is much smaller than *P. ? perditosulcata*, has a similar outline and quantity of ribs. It differs in lacking the characteristic pattern of the Portrane costellae development ; further, costellation takes place very close to the umbo, the actual style of branching not being very clear on the umbo of the type specimen. (Cooper 1956 ; pl. 50, J, figs. 45, 46).

The ornamentation of the Portrane valves immediately distinguishes them from, on the one hand, those species of *Plectorthis* which have costellae arising in virtually all rib sectors, as in *P. magna* from the Percé Formation (Cooper & Kindle 1936 : 352), and on the other, those species whose ornamentation is composed of simple costae, e.g. *P. obesa* Cooper. Other important features are the flatly convex dorsal

valve with the sulcus becoming lost anteriorly, and the comparatively strongly convex ventral valve, whose greatest depth is located umbonally. These features combine to distinguish the species from the American forms of Trenton and later age, the closest species to the Portrane form being *P. lebanonensis* Cooper, from the pre-Trenton Lebanon Formation of Tennessee. This resembles the Portrane species in outline and profile, and in the overall rib pattern. There are some differences in the ribbing however in that the costellae arise earlier, the 30 ribs already being developed by the 3 mm. stage. Moreover, there are fewer costae and more costellae, a costella being produced on sectors 3–8, with rib 1 developed late, or alternatively a costella on ribs 1–7 with an internal rib on rib 1 also, the exact relations of the middle section not being very certain from Cooper's figure of the dorsal valve (1956, pl. 81, D, fig. 15). Apart from these ribbing differences, the Tennessee form also differs in having a sulcus which extends to the anterior margin, and in possessing fine elevated threads in the inter-spaces between the ribs. These last are missing in the Lower Trenton *P. pennsylvanica* which, like *P. ? perditosulcata*, has strong concentric fila in the interspaces. This species again shows early branching on the dorsal valve which is dichotomous and not internal. It also differs from the Portrane shells in having the maximum convexity of the ventral valve at about mid-valve as well as in the presence of a persistent sulcus.

Cooper (1956 : 144) states that the genus is "not certainly known in Europe but widely identified". Of the British shells that do belong to this genus, *P. scotica*, first described by M'Coy (1852 : 232) is quite distinct from the Portrane species in its strongly biconvex profile, and the neanic dichotomous branching of its more numerous ribs. Williams (1962 : 122) recorded two valves from the Stinchar Limestone which appear to be conspecific with *P. australis* Cooper. These again show little resemblance to the Portrane shells, being ornamented by three generations of very much finer and more numerous ribs.

As Schuchert & Cooper have already remarked (1932 : 59) none of the shells ascribed by Reed (1917) to *Plectorthis* actually belongs to this genus.

The specimens from Portrane leave much to be desired, but the following rather meagre statistical data were obtained and are included for comparative purposes :

- (1) Length of ventral interarea : length of ventral valve—25, 32, 33, 34, 35% for 5 specimens.
- (2) Length : width of ventral interarea—26, 29, 30, 33%.
- (3) Ornamentation of dorsal valve—(a) at 3 mm. growth stage, 20–26 ribs developed on 1, 0, 1, 2, 2, 1, 1 valves respectively.
 - (b) At 5 mm. growth stage, 23–30 ribs developed on 1, 1, 0, 0, 1, 3, 0, 1 valves respectively.
 - (c) In counts on 21 dorsal flanks (13 left, 8 right) the frequency of the costellae was as follows : 4a⁻ (21), 3a⁻ (20), 5a⁻ (9), 2a⁻ (6), 6a⁻ (2), 4a⁻ 1⁻ (1).
- (4) Total number of ribs on complete valves, ventral and dorsal, was 26–34 on 1, 0, 4, 0, 1, 2, 0, 1, 1 valves respectively.

Plectorthis sp.

(Pl. 5, figs. 20, 21)

One dorsal valve (BB.30221) differs markedly from *Plectorthis*? *perditosulcata* in being quite strongly convex, not possessing an initial sulcus and in having a coarse costate ornamentation.

The valve is somewhat damaged, about 15 mm. long, of transversely elliptical outline, with 21-22 simple costae which have somewhat inclined sides and a rounded crest, the flat interspaces being of similar size to the ribs. At 7.5 mm. from the umbo a rib density of 4 in 4 mm. was recorded. Outline subrounded, with hingeline much less than maximum valve width, this being almost at mid-valve. Lateral profile evenly convex; interarea short, orthocline.

Internally the valve possesses a pair of long blade-like brachiophores joined posteriorly by short convergent plates to the thickened notothyrial platform; cardinal process ridge-like, possibly with a myophore at the posterior end which is damaged. Fulcral plates well developed; median ridge short, less than 2 mm.

DISCUSSION. The convexity of the dorsal valve is typical of Öpik's genus *Boreadorthis* and both radial and fine concentric ornamentation are virtually identical with his species *B. crassa* (1934 : 186) which typically possesses 18-21 ribs. The cardinalia of Öpik's species has similar brachiophores and cardinal process (p. 185, text-fig. 43) to the Portrane valve; but it apparently lacks the fulcral plates of the latter, although the figure is not clear on this point. No mention is made of fulcral plates in the text however, and as the species is placed in the Hesperorthinae and not the Plectorthinae it would appear that they are absent. The Estonian valves do differ in outline from the Portrane shell, in having a much wider hinge line which usually forms the maximum valve width. The costate species of *Plectorthis* described by Roy (1941 : 85), *P. inaequiconvexa*, differs in having a shallower dorsal valve and a greater number of ribs. Both *P. plicatella*, originally described by Hall (1847 : 122) and its variety *trentonensis* erected by Foerste (1910 : 49) for the costate forms, as typified by the Galena shale specimens figured by Winchell & Schuchert (1897, pl. 33, figs. 5-7), usually have more ribs and are very much more transverse than the Portrane specimen, whose outline is closer to the older Middle Ordovician species like *P. australis* and *P. compacta*. However, the 10 or so forms of this age described by Cooper (1956) are all ornamented by larger numbers of ribs.

Genus **HEBERTELLA** Hall & Clarke 1892

Hebertella sp.

(Pl. 5, figs. 24, 25)

This genus is only represented in the Portrane material by a single ventral valve, and possibly a dorsal valve.

DESCRIPTION. Ventral valve of (?) subelliptical outline; profile moderately convex, flattening anteriorly in lateral profile and gently arched medianly in anterior

profile. Interarea curved, apsacline ; delthyrium open. Ornamentation multicostellate. Interior with strong teeth supported by strong dental plates, continuing anteriorly as low ridges to define the muscle field. Muscle field somewhat suboval, slightly longer than wide, with the maximum width at the front of the dental plates ; edges of diductor scars almost straight and narrowing anterior to this point ; narrowly rounded in front but not enclosing the adductor scars ; adductor scars elongate, situated on a double median ridge, which has a shallow groove medianly along its length. A pair of *vascula media* rise at the anterior ends of the diductor scars.

DISCUSSION. Apart from the ventral valve described above (BB.30222), a poorly preserved dorsal valve (BB.30223) is also tentatively placed in this genus. This dorsal valve is of subelliptical outline with evenly convex anterior and lateral profiles. The anterior commissure is gently plicate ; the ornament, although poorly preserved, is similar to that of the ventral valve. Unfortunately, the internal structures are completely obliterated by siliceous material, making absolute identification impossible.

The ventral valve clearly belongs to the genus *Hebertella* in the majority of its features, although the overall shape of the scar, with the lateral edges convergent immediately anterior to the dental plates, is more reminiscent of some species of *Doleroides* than the type species of *Hebertella*, *H. sinuata* (Hall), in which the scar continues to expand for some distance beyond the dental plates (see Schuchert & Cooper 1932, pl. 11, fig. 24). There is, however, considerable variation of this feature within *Doleroides* species (see Cooper 1956, pl. 92 *et seq.*) ; the presence of the double median adductor ridge clearly separates the Portrane *Hebertella* from *Doleroides*, the scar outline being a specific character of the Portrane shell. The Portrane occurrence is the first definite record of the genus from Western Europe, but the material is at present insufficient for identification at specific level.

Genus *SCHIZOPHORELLA* Reed 1917

Schizophorella fallax (Salter) *silicis* subsp. nov.

(Pl. 5, figs. 9, 13-19, 22, 23 ; Pl. 6, fig. 1)

DIAGNOSIS. Dorsi-biconvex shells, outline varying from rounded to transversely elliptical ; cardinal angles obtuse, rounded, hinge-line width about three-quarters of maximum valve width. Ventral valve about four-fifths as long as wide, and about one third as deep as long ; interarea curved, apsacline, about one-fifth as long as wide, and one-fifth as long as valve ; delthyrium open, anterior profile evenly convex or slightly indented medianly by smoothly rounded sulcus, which passes evenly into the convex flanks, originating at about 7 mm. anterior to umbo (which may be excavated). Anteriorly the sulcus forms a median tongue which projects dorsally to varying extent ; lateral profile of valve accordingly with greatest depth towards posterior.

Dorsal valve about two-thirds as long as wide and two-fifths as deep as long,

evenly convex in lateral profile ; anterior profile swollen medianly due to rounded fold originating at about 8 mm. from umbo, normally remaining low whilst often producing a strongly developed plication in anterior commissure. Interarea flat or only slightly curved, normally orthocline, up to about one-tenth as long as valve ; notothyrium open. Ornamentation of fine, rounded to subangular costae and costellae with occasional strongly marked concentric growth stages. Density of radial ornamentation between 4 and 6 ribs per 2 mm. measured 5 mm. antero-medianly to ventral umbo, the total number of ribs at 10 mm. from the umbo being about 50-60.

Ventral interior with teeth supported by strong dental lamellae, advancing as high ridges to mark outside of elongate muscle field, which is about half as wide as long and about half as long as valve. Muscle field comprises a variably developed pedicle callist umbonally ; a narrow lanceolate adductor scar situated on a median ridge which increases in stature to the front of scar. On either side is a pair of elongate median diductor lobes, whilst lateral diductor lobes are situated off the valve floor on parts of dental lamellae adjacent to median lobes. Anterior of muscle field may be slightly indented medianly where median diductor lobes extend beyond adductor ridge. On valve floor in front of the latter is a low ridge which soon forks ; these features mark the position of the *vascula media*, which then curve round postero-laterally in an arc to surround the large, well marked scars of saccate gonocoeles.

Dorsal interior with low notothyrial platform on which is situated a swollen, ventrally grooved cardinal process. Anterior to platform a strong median ridge develops, rising abruptly, then falling to pass into valve floor by mid-valve. Brachiophores strong, blade-like, deep (being about half as deep as long), in section flattish or slightly sinuate with groove on the inside ; supported posteriorly by convergent plates which pass into notothyrial platform. Sockets defined by small fulcral plates. Smooth, poorly delimited subquadrate muscle field divided longitudinally by median ridge, with posterior adductor pair slightly larger than anterior pair ; gonocoeles strongly impressed lateral to muscle scars, and pair of *vascula media* developed anterior to scars.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30224)	. *15.3	c. 21 mm.
PARATYPES.	Dorsal valve (BB.30225).	. 16.3 mm.	22.9 mm.
	Ventral valve (BB.30226)	. *14.4 mm.	15.4 mm.
	Broken dorsal valve (BB.30227)	. —	—
	Deformed ventral valve (BB.30228)	. —	—
	Broken ventral valve (BB.30229)	. —	19.7 mm.
	Damaged ventral valve (BB.30230)	. —	—

* Ventral commissural length (see Text-fig. 1)

DISCUSSION. The new subspecies is distinguished from *S. fallax* principally by the narrower and more elongate ventral muscle field ; and to a lesser extent by the stronger median ridge of the dorsal valve.

The Portrane sample consists of 39 ventral and 35 dorsal valves ; but the nature of the preservation of these specimens is such that only meagre statistical data could be obtained for comparison with the other recorded specimens of *S. fallax*. Further, the illustrations of earlier authors are not always of value in building up data on the specific characters ; the valves ascribed to this species from the Upper Ordovician Hovin Sandstone of the Trondheim area by Reed (1932, pl. 18, figs. 3-5) may be cited as an example.

The measurement of the length of the ventral valves in the Portrane shells used in the data was taken in the plane of the commissure : due to the development of a median tongue the maximum valve length is usually in excess of this (see Text-fig. 1). For valve outline, the length : width % for five ventral valves on which measurements were possible show a mean of 82.8% (var. 76.75) ; four dorsal valves which average 64% for this character show a range of 46 to 82%. Thus while Salter's figures of a dorsal valve from Pomeroy (1846, pl. 5, fig. 3a) falls within the range for the Portrane shells, his ventral valve (fig. 3b) is more transverse ; no significance can be attached to this however.

The thickness : length % in four Portrane ventral valves is 28, 29, 31, 37% ; and in four dorsal valves 31, 34, 41 and 53%. The mean length : width % of the interareas of six ventral valves is 22.2% (var. 5.0), with a mean length of interarea : valve length of 21.75% (var. 0.9) in four valves ; the length of interarea : length of valve in three dorsal valves is 7, 9, and 10%.

The full data for the ventral muscle field is given below (p. 201) ; the mean width : length ratio is 49%, with a range of 36-62%. A comparison with the scars of other figured specimens shows that of the new subspecies to be relatively longer and narrower. As the majority of figures available are internal casts, the measurements obtained from them for the width of the scar are less than the true width of the scar. This is because the scars extend across the lower parts of the dental plates ; these diverge away from the floor of the valve, so that their tops are not visible on the internal moulds. Salter's figure 3b gives a width : length ratio of 67% ; Reed's figures 19 and 24 (1917, pl. 10) of specimens from the Upper Drummuck at Girvan are conservatively estimated at 60 and 64% respectively ; while Schuchert & Cooper figure an internal mould with a ratio of about 67% (1932, pl. 12, fig. 1). A cast taken from this last (pl. 12, fig. 9) shows a ratio of about 76%, some of the shortening being due to the tilted attitude of the specimen. These values, although, as stated, underestimated for the moulds, are still higher than the figures for the Portrane subspecies, indicating the narrower nature of the scar in the latter.

The other feature by which the new subspecies can be distinguished from the Pomeroy and Girvan shells is the dorsal median septum, which is generally much stronger in the Portrane shells. In two complete shells it extends for 40 and 52% of the valve length.

No differences were established between the new subspecies and *S. fallax* s.s. as

regards shell shape or ornamentation. Three Portrane ventral valves showed a total of 48, 54 and 61 ribs at 10 mm. from the umbo ; a dorsal valve also showed 61 ribs at this distance, whilst at 5 mm., two valves showed 28 and 32 ribs. The numbers of ribs per 2 mm. medianly at 5 mm. from the ventral umbo were 4, 4, 5, 6, 6 on five valves.

Apart from *Orthis mullochensis*, which was originally placed in the genus by Reed (1917 : 859) but was later shown to belong to *Mendacella* (Schuchert & Cooper 1932 : 62), the only other species to be attributed to this genus is the Russian form *Schizophorella kasachstanica*. Amongst the external differences separating this species from the type species are, according to Rukavishnikova (1956 : 120), the transversely elongate shape of the shell, the more convex ventral valve, and the distant nature of the ribbing ; and internally the thicker dental plates and the absence of the short median septum in the dorsal valve. This last point is certainly noteworthy, and an examination of Rukavishnikova's figures suggests that the species does not in fact belong to the genus *Schizophorella*. For whilst Rukavishnikova's figured ventral internal mould (pl. 1, fig. 4a) would seem very close to that of Reed's genus, the dorsal internal mould (pl. 1, fig. 4b) shows no sign of the convergent supporting plates or of the fulcral plates characteristic of the genus. Although the plate figures are not very clear, the absence of these structures is confirmed from the serial sections figured by Rukavishnikova in Text-fig. 1.

The following statistical data were obtained in a bivariate analysis of the length (l) : width (w) of the ventral muscle scar :— $n=11$; \bar{l} (var. l)=7.02 mm. (2.84) ; \bar{w} (var. w)=3.43 mm. (0.71) ; $r=0.821$; a (var. a)=0.4994 (0.00903).

Genus *SCAPHORTHIS* Cooper 1956

Scaphorthis sulcata sp. nov.

(Pl. 8, figs. 3, 4, 8-10, 13)

DIAGNOSIS. Transverse ventri-biconvex shells, of roundedly subrectangular to almost semicircular outline. Cardinal angles slightly obtuse, with maximum valve width varying in position from just anterior to hinge-line to about mid-valve ; hinge-line width over four-fifths of maximum valve width. Ventral valve almost half as deep as long, evenly convex in anterior profile, with no tendency for peripheral flattening, and only a suggestion of a fold ; convexity of lateral profile more pronounced near umbo. Interarea curved, apsacline, about one-fifth as long as valve, and slightly less than one-fifth as long as wide ; delthyrium open. Dorsal valve gently convex, with wide shallow sulcus developing medianly immediately anterior to convex umbo, separated by convex areas on either side from the flattened postero-lateral regions. Interarea very short, flat, anacline ; notothyrium small, occupied by myophore. Ornamentation of costae and costellae, together with very pronounced growth lines at intervals of about 0.1 mm., producing a reticulate appearance. Median rib of ventral valve prominent in young stages. Margins of

dorsal sulcus formed by costa 3, sulcus usually containing 6 or 8 ribs at the 2 mm. growth stage ; rib density of 3-5 ribs per mm. at this growth stage.

Ventral interior with teeth supported by weak, receding dental lamellae ; poorly defined muscle field small, triangular, somewhat longer than wide ; pedicle callist present. Dorsal cardinalia about half as long as wide approaching one-third of valve length in young stages but becoming relatively shorter in larger valves. Cardinal process slender, clearly differentiated into myophore and shaft. Brachio-phores short, blunt, with supporting plates convergent on to median ridge ; sockets defined by small fulcral plates. Median ridge simply an internal expression of sulcus, without additional thickening. Muscle field and pallial markings poorly preserved.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30258)	6.4 mm.	8.3 mm.
PARATYPES.	Damaged ventral valve (BB.30259)	c. 7.0 mm.	9.1 mm.
	Dorsal valve (BB.30260)	c. 3.5 mm.	5.1 mm.
	Broken dorsal valve (BB.30261)	5.0 mm.	—
	Broken dorsal valve (BB.30262)	7.3 mm.	—
	Unfigured damaged dorsal valve (BB.30263)	5.1 mm.	6.7 mm.

DISCUSSION. The new species is placed in the genus *Scaphorthis* on the assumption that it possesses an impunctate shell. There is, however, a little uncertainty over this point, as amongst the sample of about 30 shells there is a single specimen (BB.30263) which appears to be endopunctate when the inside of the shell is moistened ; it seems more likely that the dark spots are in fact produced by particles of mud in the external " pits ", formed by the fine reticulation of the marked growth lines with the radial ornament. Further, the " punctation " is by no means as definite as that seen in the figured specimen of *Laticrura* (Pl. 11, fig. 19) which takes the form of very clear pitting on the inside of the shell ; this preservation is rather exceptional, for no punctation has been observed in the other associated endopunctate stocks such as *Dicoelosia* and *Dalmanella*. The punctation of the shell of *S. sulcata* is then rather unlikely although this point cannot be completely resolved until sections have been taken from specimens preserved in the form of calcareous shells.

In the dalmanelloid appearance of the shell and the style of the cardinalia the species is similar to the plectorthid genera *Corineorthis* and *Giraldiella* as well as *Scaphorthis*. The convexity of the ventral valve separates the Portrane shells from *Corineorthis*, which possesses a concave ventral valve (Stubblefield 1939 : 67), and from *Giraldiella* in which the dorsal valve is more convex (Williams 1951 : 91). Species of the latter genus also differ in having an undifferentiated cardinal process.

The new species is quite distinct from the other species at present ascribed to *Scaphorthis*. The measurements given for these species by Cooper (1956 : 504-506),

converted to percentages, and arranged in ascending order, are compared with the Portrane sample as follows :—

(1) *Length : width of ventral valves.*

S. sulcata, 7 valves—59, 64, 65, 66, 77, 78, 81%.

S. kayi, 4 valves—89?, 91, 91, 92%.

S. perplexa, 3 valves—85, 89, 90%.

S. virginensis, 4 valves—86, 90, 91, 91%.

Comparison by Rank Sum Test indicates that the Portrane shells are significantly more transverse in all cases ($P=0.003, 0.008, 0.003$ respectively).

(2) *Hinge-width : valve width.*

S. sulcata, 6 valves—79, 84, 85, 87, 89, 92%.

S. kayi, 4 valves—65, 65, 69, 79?%.

S. perplexa, 4 valves—66, 69, 71, 73%.

S. virginensis, 6 valves—75, 75, 78, 80, 83, 84%.

Comparison by Rank Sum Test reveals that the hinge-line width relative to the valve width is significantly larger in *S. sulcata* than in the American shells ($P=0.007, 0.005, 0.011$ respectively).

The new species differs from the American species of *Scaphorthis* also in the development of strong closely-set growth lines which give a reticulation to the shell surface, although it is seldom preserved over the entire shell.

The Portrane dorsal valve is characterized by a wide, well-defined although shallow, sulcus which is more reminiscent of the Llandovery *Giraldiella protensa* (see Williams 1951, pl. 3, fig. 9) than of any of the American species. The mean width of the sulcus measured at 2 mm. anterior to the beak in 9 valves is 2.1 mm. (var. 0.102).

Additional data for the small Portrane samples are as follows. The thickness : length ratios of 4 ventral valves are 40, 44, 44, 45% ; four ventral valves possess interareas whose length : width percentage is 15, 17, 19, 19% and whose lengths relative to the valve lengths are 18, 20, 22, 24%.

A sample of 5 dorsal valves has a mean of 62% (var. 98) for the length : width ratio. Internally, 4 valves show a length : width ratio for the cardinalia of 46, 53, 54, 55% ; and ratios of 19, 20, 28 and 32% for the length of the cardinalia : valve length, the two smaller figures being those of the two larger valves of this sample.

The density of ornament at the 2 mm. growth stage is 3–5 ribs per mm. on 2, 4, 4 dorsal valves respectively. At this growth stage a distribution of 6–10 ribs in the sulcus occurs in 4, 1, 3, 0, 1 valves respectively. The ribs present here are 3a-, 2, 1 on either side of the median line, variously supplemented by the development of an internal costella on sectors 1 and 2. Details of the order of insertion of the ribs are given in Table 5.

Rib counts on the ventral valve at the 2 mm. growth stage reveal 18, 21, 22, 24, 25 ribs on 5 valves ; and at the 5 mm. growth stage 3 valves possess 39, 41 and 45 ribs.

TABLE 5

Rib relation	Frequency
2a ⁻) 3a ⁻ . . .	0/8 (1)
2a ⁻) 4a ⁻ . . .	1/5
2a ⁻) 2a ^o . . .	4/4
3a ⁻) 3a ^o . . .	11/11
3a ⁻) 4a ⁻ . . .	10/10
3a ⁻) 4a ^o . . .	1/6 (3)
3a ⁻ 1 ⁻ a ⁻) 2a ^o . . .	2/2
3a ⁻ 1 ⁻ a ⁻) 3a ^o . . .	2/2
4a ⁻) 4a ^o . . .	0/7
4b ⁻) 4b ^o . . .	0/5

TABLE 5. Table showing the frequencies of relative costella development on dorsal valves of *Scaphorthis sulcata* sp. nov. Figures in parentheses denote the frequency of forms in which the ribs involved arose simultaneously.

Subfamily **RHACTORTHINAE** Williams 1963

Genus **RHACTORTHIS** Williams 1963

Rhactorthis sp.

(Pl. 8, figs. 1, 2, 5-7)

DESCRIPTION. Subcircular ventri-biconvex shells possessing a sulcate anterior commissure. Ventral valve about two-fifths as deep as long, evenly convex in lateral profile and slightly carinate in anterior profile; interarea curved, apsacline, about a quarter as long as wide and a quarter as long as the valve; delthyrium open. Dorsal valve four-fifths as long as wide and almost one-third as deep as long, evenly convex in lateral profile but grooved medianly in anterior profile by a rather narrow sulcus arising just in front of the umbo; this becomes broader and shallower towards the front and may be almost lost except as an undulation in the anterior commissure. Dorsal interarea very short, orthocline to slightly apsacline, notothyrium partially filled by the myophore. Ornamentation consisting of hollow costae and costellae, dorsal valve with just over 30 ribs developed at the 3 mm. growth stage, and a density of 3 per mm. at the 5 mm. growth stage; distinctive concentric ornamentation of strong, irregularly spaced and exaggerated "growth lines".

Ventral interior with teeth supported by short dental lamellae bounding the postero-lateral sides of the muscle field; this is sub-triangular in outline, with length and width about equal, and divided into a broad adductor track flanked by slightly longer submedian diductor lobes. Dorsal interior with cardinalia consisting of cardinal process with crenulated myophore and thick shaft which is continuous with a stout median ridge extending to about mid-valve; adductor field divided longitudinally by the median ridge; *vascula media* and *vascula myaria* radially arranged.

Figured Specimens	Length	Width
Dorsal valve (BB.30264) . . .	5.3 mm.	c. 6 mm.
Dorsal fragment (BB.30265) . . .	c. 7.5 mm.	—
Ventral valve, broken marginally (BB.30266)	—	—

DISCUSSION. The Portrane species possesses all the typical characters of Williams' genus (1963 : 371). The Irish shells show much closer affinity to the type species, *Rhactorthis crassa*, than to *R. melmerbyensis* (Reed 1910 : 296), the only other species so far attributed to the genus. Reed's species differs from the Portrane species and *R. crassa* in possessing a strongly carinate ventral valve. The thickness : length ratio is also larger, varying from 42 to 56% in the 3 shells cited by Williams (1963 : 375) compared with 37 and 38% for 2 Portrane shells.

The genus is uncommon in the Portrane material, only 7 specimens in varying states of preservation being available for comparison with the type species.

The thickness of the ventral valves is almost identical, although the figure of 30% for thickness relative to valve length for a single Portrane dorsal valve is deeper than the mean of 22.2% (var. 8.2) for 6 Welsh shells. A Portrane dorsal valve shows a length : width ratio of 81% compared with a mean of about 72% for the Welsh sample. This statistic for 3 ventral valves is 76, 83, 91% ; no data are given by Williams for this feature. The length : width of the cardinalia are 48, 50 and 53% in 3 Portrane valves, higher than the mean (c. 41%) for the Welsh valves, as is the length of the cardinalia relative to the valve length (21% in 2 Portrane valves, and a mean of c. 17½% for *R. crassa*).

The density of 3 ribs per mm. at 5 mm. from the dorsal umbo on one Portrane valve is the modal number for the type species. Due to adherent silica, rib counts were not obtained at the 2 mm. growth stage, but at 3 mm., where 31, 32, 33 were counted on three valves.

While the Portrane shells are similar to *R. crassa*, they appear to differ in having a less transverse outline, a deeper dorsal valve and relatively longer cardinalia. However, with the very small amount of data available, the Portrane shells are placed as *Rhactorthis* sp., at least until further material is obtained to ascertain the true significance of these differences.

Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene 1929

Genus **PLATYSTROPHIA** King 1850

Platystrophia lutkevichi Alichova *contemplata* subsp. nov.

(Pl. 6, figs. 7, 10–16, 18)

1861 *Orthis biforata* Schlotheim ; Baily : 11 (*pars*).

1880 *Orthis biforata* Schlotheim ; Baily : 82 (*pars*).

1895 *Orthis biforata* Schlotheim ; Sollas : 101 (*pars*).

DIAGNOSIS. Differs from *P. lutkevichi* Alichova, as restricted by Oraspöld (1959 : 54), in having relatively shorter hinge-line and wider sulcus, and attaining larger size, with which is associated the development of additional ribs on the fold and in the sulcus.

DESCRIPTION. Strongly biconvex shells of subquadrate outline ; maximum width at about mid-valve, hinge-line varying from three-fifths to three-quarters of the maximum width. Ventral valve with length (measured in the plane of commissure) ranging from six to nine-tenths of the valve length ; maximum valve length may be up to 10% longer, dependent on convexity ; interarea short, curved, apsacline, about one-ninth of the valve length ; that of the dorsal valve slightly shorter ; curved anacline. Ventral sulcus deep with flattish sides and bottom, maximum width at anterior margin just over half of the valve width ; corresponding dorsal fold prominent, flat-topped. Ornamentation of strong angular costae, with between 6 to 9, most commonly 7 or 8, on each flank at the 5 mm. growth stage ; this may increase to a maximum of 10 at later stages by development of additional costae along the hinge-line. Sulcus with two ribs umbonally, usually increasing by implantation of a rib on each flank and internal branching of the initial pair to produce six ribs in the sulcus of adult valves, with one or two additional ribs appearing in the largest shells. Dorsal fold with three ribs in young stages, normally with external costellae developed on the outer pair, with branching on either side of the median costa in later growth stages.

Ventral interior with moderately strong teeth and strong dental lamellae, advancing to delimit the thickened, elongated suboval muscle field which is about two-fifths of the valve length, with a slightly larger mean for the ratio width : length of the scar itself (for 9 valves the figure is 42·7% (var. 47·4)). Dorsal interior with strong tusk-like brachiophores, small sockets defined by fulcral plates, and a fairly high plate-like cardinal process on the notothyrial floor ; posterior adductor scars smaller than anterior, other details of muscle scars and pallial markings not visible in this material.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30231).	17·8 mm.	20·3 mm.
PARATYPES.	Ventral valve (BB.30232)	15·4 mm.	25·1 mm.
	Dorsal valve (BB.30233).	c. 20 mm.	22·7 mm.
	Damaged dorsal valve (BB.30234)	—	—
	Dorsal fragment (BB.30235)	—	—
	Ventral fragment (BB.30236)	—	—
	Dorsal fragment (BB.30237)	—	—

DISCUSSION. Since the erection of *Platystrophia* by King (1850 : 106), much has been written on this genus which was of widespread distribution and common occurrence from Middle Ordovician to Middle Silurian times. The first extensive analysis of the genus was carried out by Cumings (1903 : 10), who recognized the three basic subdivisions of uniplicate, biplicate, and triplicate types, currently referred to as the unicostate, bicostate and tricostate groups (Schuchert & Cooper 1932 : 67) ; these group names refer to the numbers of radial ribs in the ventral sulcus at the completion of the early growth stages of the shell.

In the Portrane sample, 1-3 costae are present in the ventral sulcus of 2, 35 and 1 valves respectively at the 5 mm. growth stage. The valve with 3 ribs was a

bicostate form in the younger stages, having a median rib intercalated later. The two specimens with a solitary rib, would, if not found associated with the bicostate shells, be termed unicostate forms and be included in a different species group ; however these appear to be natural variants of the population, for as Cumings says (1903 : 11), " practically any group of *Platystrophia* may produce an occasional uniplicate individual ".

McEwan (1920) elaborated on the basic subdivisions of Cumings and the bicostate group, to which the Portrane shells belong, was divided into four subgroups, again on the basis of rib development on the fold and sulcus (p. 389). Subgroup A possesses two costae in the sulcus and three on the fold ; subgroup B has an extra costa intercalated medianly between the two costae of the sulcus, whilst the median rib of the fold bifurcates ; subgroup C has a costa developed on the lateral slopes of a style A sulcus, whilst the two lateral costae of the fold both bifurcate ; subgroup D is a combination of B and C, so that the sulcus has the basic two costae with the addition of both a median and a pair of lateral ribs, whilst on the fold all three ribs bifurcate. The presence in the Portrane sample of shells showing the typical development of subgroups A, C and D, suggests that, although variability of rib development was known to McEwan, not sufficient consideration was given to this facet in the development of her " pigeon-hole " classification.

The artificial nature of McEwan's classification has also been pointed out by Williams (1962 : 126), after examination of topotype material of some of McEwan's Trenton " species " ; again, in a description of the Bala specimens of *Platystrophia* (Williams 1963 : 371) difficulties similar to those appertaining to the Portrane shells were experienced, i.e. what is certainly a homogeneous sample would have to be split into three or more species using McEwan's system of classification.

Many of the Portrane shells are broken anteriorly, so that in most cases it is only possible to determine the number of costae in the sulcus or on the fold at the 5 mm. growth stage ; the figures for the ventral sulcus have been given above, for the dorsal fold 3, 40 valves have 2, 3 costae respectively, the frequency of " unicostate " forms being similar to that found in the ventral valve. At the 10 mm. growth stage, 3 and 4 ribs are present in the ventral sulcus of 5, 4 shells, and at the 15 mm. stage 5 and 6 ribs are present in 1 and 3 valves respectively. One large fragment shows 8 ribs in the sulcus. Of the larger specimens, 8 show the development of a rib on each lateral slope of the sulcus as the first stage of rib increase (subgroup C), although the pair do not always appear simultaneously, and the appearance of the first may vary anywhere from between about 6 and 10 mm. anterior to the umbo. At a later stage (10-14 mm.) 5 of these show the development, again not always symmetrical, of an internal branching of the two initial ribs in the sulcus. In three other shells, a single median rib arises before the development of the lateral pair (subgroup D, but which would also be classified as subgroup B had the shells ceased growing before the appearance of these lateral ribs), in one specimen as an intercalated rib, in the others as the internal branch of one of the initial ribs. In the large fragment mentioned above, the two lateral ribs are the first to develop after the initial pair in the sulcus ; subsequently the right-hand rib of the original pair

branches internally, followed by the appearance of a second pair of lateral ribs at the side of the sulcus, and an internal branching of the first lateral rib on the left-hand side to produce a total of eight ribs in the sulcus at the anterior margin (Pl. 6, fig. 7).

The number of ribs in the sulcus of the Portrane shells depends then to a certain extent on the size attained by the valves ; the pattern is basically bicostate, most frequently of subgroup C style, with the addition of a pair of internal ribs developing from the two initial costae.

The pattern on the dorsal fold is complementary to this ; in three valves the outside pair of the basic three ribs branch externally to produce 5 ribs at the 10 mm. growth stage ; in the specimen which attains 15 mm. in length, 7 ribs are present by that stage, the additional pair arising on either side of the median rib. A single valve resembles the styles of the subgroups B and D, the median rib bifurcating, with an external rib rising on one of the lateral ribs later.

The mean wavelength of the costa immediately lateral to the sulcus on 8 ventral valves at 10 mm. from the umbo is 1.32 mm. (var. 0.0157).

The style of ornamentation of the Portrane valves compares broadly with only four of the many described forms of the genus ; *P. fissicostata* (M'Coy), *P. camerata* Twenhofel, *P. lutkevichi* Alichova and its subspecies *P. lutkevichi satura* Oraspöld.

From M'Coy's description of *P. fissicostata* (1852 : 193), it is evident that his "specific characters" are the summation of characters observed in a large number of what would now be regarded as distinct stocks, and which had as a common theme the general appearance of *P. biforata* with the ribs branching somewhere on the shell. Undoubtedly a large quantity of *Oxoplecia* were present in this material, as well as various *Platystrophia*s of Caradocian and Ashgillian age.

This species is in dire need of reassessment. Of the specific characters given by M'Coy, only the description of the ventral sulcus is of any consequence, and it is from this that the characters of the species must be re-assessed :—"four ribs on the rostral part of the mesial furrow, the two outer of which usually branch at four or five lines from the beak, the others branch irregularly lower down once or twice". This style of ornamentation is seen in the specimen from Llanfyllin figured by Davidson (1869, pl. 37, fig. 19). The presence of four ribs in the sulcus at an early stage is very similar to *P. camerata*, and quite different from the Portrane shells, where the two initial ribs persist by themselves for some distance to give a totally different appearance to the sulcus. All the characters of the species cannot be assessed from Davidson's figure 19 ; but in the number of ribs on the flanks, the apparently flat-bottomed and sharp-sided sulcus it resembles the Portrane shells, differences being observed in the relatively narrower sulcus, the wider hinge-line (85% of maximum valve width), and the protruding tongue of the sulcus in the Welsh shell (which may be due however to the orientation of the shell).

The only American shell which shows close similarity to the Portrane form is *P. camerata* described by Twenhofel (1928 : 178) from the Ellis Bay Formation of Anticosti. Whilst this is indistinguishable from the Irish shell in many features (e.g. outline, length of hinge), it differs in the following :—(1) The fold is rounded, with the sides passing evenly into the flanks instead of having abrupt margins as

on the folds of the Portrane shells ; (2) For the ratio of maximum width of sulcus : maximum valve width, 41% was obtained from Twenhofel's measurements for a shell, and 44% for his figured specimen, compared with 53, 53 and 55% for three Portrane valves ; (3) While the ribs on the flanks would appear to be similar in number (c. 10), those on the Anticosti shells produce costellae, some of which are developed within the size range of the slightly smaller Portrane shells (see Twenhofel 1928, pl. 15, fig. 13) ; (4) The development of lateral ribs in the sulcus takes place earlier. In the Portrane shells these generally do not appear simultaneously, and although, as stated above, the appearance of the first may vary from about 6 to 10 mm., the mean for seven specimens is 8.6 mm. (var. 2.7) ; and in the specimen where the first rib rises early at 5.9 mm., the one on the opposite side does not appear until 8.8 mm. In Twenhofel's species the lateral ribs appear at "about 7 mm.". From Twenhofel's figure (pl. 15, fig. 15), although this distance cannot be measured, it is evident that the lateral ribs strengthen very quickly, unlike the later laterals of the Portrane shells.

P. lutkevichi was recorded by Alichova (1953 : 26) as coming from the Wesenberg (E) and the Saaremuusa (Fr) strata of the Leningrad region. Oraspöld, working on the Estonian Ordovician, found differences between the Platystrophias of the different ages, and erected a new subspecies (1959 : 53) for the specimens occurring in both substages ($F_{1a\alpha}$ and $F_{1a\beta}$) of the Nabala Stage (Männil 1958 : 4). This subspecies differs from the Wesenberg shells in possessing from 12 to 17 ribs on the flanks of the ventral valve, more ribs also on the fold and in the sulcus, and, according to Oraspöld (1959 : 54), in having the width at the posterior margin and at the middle almost equal. This last is in contrast to the Wesenberg shells where the greatest width is at the middle of the shell ; but the figures of both *P. lutkevichi* s.s. (Alichova 1953, pl. 1, figs. 10, 11 ; Oraspöld 1959, pl. 1, figs. 3-5) and *P. lutkevichi satura* (Alichova, pl. 1, figs. 9, 12 ; Oraspöld, pl. 1, figs. 1, 2) show forms which resemble the other subspecies in this respect.

The great number of ribs on the flanks of *P. lutkevichi satura* and on the fold (12) and sulcus (11) at the anterior commissure, also readily distinguishes this subspecies from that of Portrane, as does the very wide hinge-line of the Baltic form (Oraspöld's figures (1959 : 53) give ratios of 90, 93 and 96% compared with 58, 64, 70, 71 and 75% for 5 Portrane shells) and the low nature of its fold in adult shells (Oraspöld 1959, pl. 1, fig. 1a).

P. lutkevichi s.s. differs from *P. camerata* and *P. fissicostata* and resembles the Portrane species in the persistence to mid-valve of the two initial ribs of the sulcus by themselves (see Oraspöld 1959, pl. 1, figs. 3, 4), with later ribs of similar pattern which do not attain the size of the earlier ones until the anterior margin (Alichova 1953 : 26). Other similarities to the Portrane valves are found in the range of the ribs developed on the ventral flanks (8-11), the steep-sided fold and the flat-bottomed sulcus. Differences may be seen in the wide hinge, which, although it represents the maximum valve width in some Leningrad forms (Alichova 1953, pl. 1, fig. 10), is only about 79 and 80% for the two complete Estonian valves figured by Oraspöld (1959, pl. 1, figs. 3, 4) ; and also in the narrower sulcus (about 45% of maximum valve width measured anteriorly at its top).

The present writer regards these differences in shape as being of lower taxonomic value than the other features, and accordingly the Portrane shells are placed in *P. lutkevichi*, as a separate subspecies.

Genus **MCEWANELLA** Foerste 1920

Mcewanella dorsisulcata sp. nov.

(Pl. 6, figs. 17, 19-21 ; Pl. 7, figs. 1-4)

DIAGNOSIS. Ventri-biconvex shells usually of transverse outline, but showing large variation in shell shape ; hinge-line normally less than maximum valve width, which is located a short distance anterior to it ; cardinal angles usually rounded, obtuse. Ventral valve with median fold ; interarea curved, apsacline, about one-sixth of valve length ; delthyrium open. Dorsal valve with deep median sulcus extending the length of valve and shallowing slightly ; interarea orthocline, flat or very gently curved, half the length of that of ventral valve ; notothyrium open. Ventral valve initially with 7-9 angular costae, basic pattern consisting of median rib flanked by three on either side, with variable occurrence of pair of outside ribs, which curve round to terminate against posterior margin. The other costae usually give rise to single external costella on each between the 3 and 6 mm. growth stages ; between the 7 and 11 mm. growth stages, often after pronounced break in growth, fine costellae develop on earlier ribs. These costellae may or may not be produced simultaneously on all ribs. Dorsal exterior with 8-10 initial costae, most commonly 8, median 2 lying in sulcus ; mean wavelength of costae, measured medianly at 3 mm. from umbo, for a sample of 8 shells is 0.94 mm. (var. 0.034). Strong concentric growth lines and breaks present at irregular intervals.

Ventral interior with strong teeth and dental lamellae continuing anteriorly as ridges to bound the sub-rectangular muscle field, which is about one-third as long as valve, and about two-thirds as wide as long. Adductor scar over one-third of the width of whole scar, usually terminating slightly posterior to diductor scars, with its anterior portion on thickened ridge in older valves. Dorsal cardinalia with cardinal process composed of well-developed myophore and strong shaft ; short brachio-phores, curving ventrally to produce tusk-like appearance, with supporting plates which extend vertically to valve floor ; fulcral plates well developed, bounding small sockets, and defining deep crural pits. A pair of low ridges extend antero-medianly from front of supporting plates to meet at almost middle of subquadrate adductor field ; this muscle field with maximum length medianly, half as long as valve, and between half and three-quarters as wide as long.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30238)	14.9 mm.	22.5 mm.
PARATYPES.	Ventral valve (BB.30239)	12.4 mm.	15.4 mm.
	Dorsal valve (BB.30240).	14.6 mm.	13.0 mm.
	Dorsal valve (BB.30241).	—	16.4 mm.
	Ventral fragment (BB.30242)	—	—
	Ventral fragment (BB.30243)	—	—
	Damaged ventral valve (BB.30244)	c. 15 mm.	—

DISCUSSION. Although some ninety valves of this species have been recovered, they are mostly fragmentary and generally show an inordinate amount of adhering silica. Thus only sparse statistical data were obtained, in spite of the relative abundance of the form. For the shell outline, a sample of 7 ventral valves showed a mean length : width ratio of 71.4% (var. 242.3). This large variation in outline is equally well shown for the dorsal valves, where ratios of 112, 98 and 74% were recorded for three valves. Whilst many specimens show tectonic deformation, both transverse and more elongate shells are present which have not suffered any noticeable post-depositional distortion. The development of costellae is also dependent to a certain extent on shell outline and accordingly also shows considerable variation; e.g. at the 10 mm. growth stage a transverse ventral valve showed 33 ribs, whilst one which was just slightly wider than long possessed only 19 ribs.

Prior to the discovery of this new species, only three species of the genus were known. Of these, two, *M. lineolata* Savage and *M. raymondi* Foerste are North American forms of Richmond and Trenton ages respectively, although there seems to be some doubt over this latter age (Schuchert & Cooper 1932 : 70). The third species, *M. berwynensis*, was described from the Upper Llandeilo beds of North Wales by MacGregor (1961 : 183) ; although this is a much earlier form, it shows a greater affinity to the Portrane species than the American shells in the possession of a dorsal, not ventral, sulcus.

The Portrane shells differ from *M. berwynensis*, however, in having a cardinal process which is composed of a myophore and shaft, unlike the simple ridge of the Welsh species. A simple ridge is more typical too of the American shells, although they do sometimes show a distinct, but rather slender, myophore (Cooper, 1944, pl. 112, fig. 58). Again in contrast to the other species, *M. dorsisulcata* possesses supporting plates which extend vertically to the valve floor, instead of converging to unite beneath the cardinal process.

Externally the dorsal sulcus is much stronger than in *M. berwynensis*, while the two median ribs are, if anything, less prominent than the ones lateral to them. The number of initial costae in the Portrane dorsal valves was 8 to 10, in 8, 2, and 1 shell respectively, the mode being 2 less than the figure given for MacGregor's species (p. 183) ; whilst in the ventral valves 7 to 9 ribs were recorded for 6, 4, and 5 valves, 9 also being recorded for *M. berwynensis*. Later costellae development in the two forms is strikingly different ; for whereas in *M. berwynensis* (MacGregor 1961, pl. 19, figs. 9-15), and also in *M. raymondi* Foerste (1920, pl. 23, fig. 1), the original costae become covered with fine radiating costellae, in the Portrane shells strong "normally branching" external or internal costellae develop, long before the fascicles of costellae so typical of the genus, which generally tend to be slightly coarser and accordingly less numerous than in the other species.

The new species may be most readily recognized by the strong sulcus of the dorsal valve, the style of costellation and the features of the cardinalia.

Family **SKENIDIIDAE** Kozłowski 1929Genus **SKENIDIOIDES** Schuchert & Cooper 1931***Skenidioides* cf. *asteroidea*** (Reed)

(Pl. 7, figs. 5-13)

1917. *Scenidium Lewisi* Davidson, var *asteroidea* Reed: 921, pl. 22, figs. 1-3.

DESCRIPTION. Sub-pentagonal *Skenidioides* with maximum width just anterior to the hinge-line, cardinal angles over 90° . Posterior edges of the valve not parallel to the hinge-line, but forming a straight-sided obtuse angle at the umbo; laterally and anteriorly the outline is evenly rounded. Ventral valve almost four-fifths as long as wide, and half as deep as long, with only a weakly developed median fold. Anterior profile evenly convex, with a tendency to flatten slightly laterally; lateral profile variable, from low pyramidal with a gently convex surface to forms of dalmanellid aspect which are quite strongly convex with somewhat incurved beaks. Interarea well developed, about two-fifths of the valve length, curved or flatly apsacline. Dorsal valve flatly to gently convex; median sulcus broad, evenly and gently rounded. Ornamentation of even, sub-rounded ribs; ventral fold usually with fascicle of 2-4 ribs by 3 mm. distance from the umbo, a solitary median rib being unusual. External costellae (normally $2a^\circ$) also developed by this stage, the total ribs ranging from 12-21. Rib wavelength at the 2 mm. growth stage about one third mm. Dorsal valve with internal costellae, never more than one costella per sector.

Ventral interior with a spondylium over one-third of the valve length. Dorsal cardinalia with simple cardinal process; sockets bounded by fulcral plates; brachioophores long, slender, the bases converging on to the median septum at almost one-third of the valve length, the septum itself extending for three-quarters of the valve.

Figured Specimens	Length	Width
Ventral valve (BB.30250) . . .	5.5 mm.	6.8 mm.
Dorsal valve (BB.30251) . . .	4.2 mm.	5.5 mm.
Dorsal valve (BB.30252) . . .	2.9 mm.	4.1 mm.
Ventral valve, damaged marginally (BB.30253)	—	c. 10 mm.
Ventral valve (BB.30254) . . .	4.2 mm.	—

***Skenidioides paucicostatus* sp. nov.**

(Pl. 7, figs. 14-20, 22, 25, 27)

DIAGNOSIS. Transverse, alate *Skenidioides* with maximum width along hinge-line; valve outline with concave posterolateral margin becoming convex anterolaterally, whilst the front may be straight, protruding or embayed. Ventral valve about half as long as wide, and half as deep as long, bearing well-defined median fold; anterior profile thus strongly convex medially, lateral profile gently convex, becoming strongly convex anteriorly in some of the older valves (length about

4 mm.). Dorsal valve moderately convex with deep, steep-sided median sulcus. Ornamentation of subangular costae with, in ventral valve, strong median rib whose wavelength at 2 mm. from the beak is almost 0.8 mm., flanked on either side by three smaller but still prominent ribs (wavelength almost 0.5 mm.), outside which may occur from 1-3 fine costae. Median rib occasionally bifurcating; costellae only exceptionally developed. Dorsal valve with 3 strong ribs on either side of sulcus, usually with finer one lateral to them.

Interior of ventral valve with spondylium which extends about one-third of valve length, only supported by septum posteriorly; dorsal cardinalia consisting of simple ridge-like cardinal process passing anteriorly into strong median septum. Septum extending for about three-quarters of valve length. Brachiophores small, supported by bases which converge onto median septum at about one-third of valve length anterior to umbo; sockets small, defined by fulcral plates.

		Length	Width
HOLOTYPE.	Ventral valve (BB.30245)	3.7 mm.	—
PARATYPES.	Ventral valve (BB.30246)	2.5 mm.	4.55 mm.
	Ventral valve (BB.30247)	2.1 mm.	4.8 mm.
	Dorsal valve (BB.30248).	2.0 mm.	—
	Dorsal valve (BB.30249).	2.9 mm.	—

DISCUSSION. Whilst *Skenidioides* is a commonly occurring genus in the Portrane fauna, 235 ventral and 128 dorsal valves being recovered, the majority of the specimens are too fragmentary to contribute much to the description of the species.

The shells belong to two distinct species, *S. paucicostatus* sp. nov. and *S. cf. asteroidea* Reed. The former is transverse and alate, with a few coarse subangular costae and seldom any costellae, a sharp dorsal sulcus, and ventral fold whose median rib is much stronger than the remainder. The latter differs in being of sub-pentagonal outline, with a higher interarea, less angular ribs with costellae developed, and a gentle fold and sulcus on which the ribs are of even size. Data obtained for the two species is compared as follows:—

Length (l) : width (w) of ventral valve.

		<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
n	.	17	16
l (var. l)	.	4.34 (3.602) mm.	2.83 (0.708) mm.
w (var. w)	.	5.56 (5.362) mm.	5.96 (2.361) mm.
r	.	0.9012	0.8525
a (var. a)	.	1.220 (0.01888)	1.826 (0.06507)

A comparison of the valve outlines from the above statistics shows *S. paucicostatus* to be significantly more transverse than *S. cf. asteroidea* ($.05 > P > .02$). The adult *S. paucicostatus* does not attain the length of the larger *S. cf. asteroidea*; but growth-lines on the latter indicate that the sub-pentagonal shape is maintained throughout growth, so that there is no chance of *S. paucicostatus* being simply the young of the other species in the same way that the auriculate young forms of *S. obtusus* develop rounded cardinal extremities in later life (Cooper 1956 : 497).

Length (l) : thickness (t) of ventral valve.

	n	.	.	.	<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
					14	18
l (var. l)	4.46 (2.424) mm.	2.98 (0.723) mm.
t (var. t)	2.24 (1.028) mm.	1.43 (0.180) mm.
r	0.8584	0.8561
a (var. a)	0.6512 (0.009298)	0.499 (0.004158)

A comparison of the two species reveals no significant differences in either the *a* or *b* values for valve profile.

Length of valve (l) : length of ventral interarea (ia).

The impression of greater length of the interareas in *S. cf. asteroidea* may in fact be due to the greater overall size of those valves when compared with *S. paucicostatus*; accordingly data were taken in order to compare the growth rates for the two samples.

	n	.	.	.	<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
					28	34
l (var. l)	4.50 (2.313) mm.	3.03 (0.670) mm.
ia (var. ia)	1.79 (0.513) mm.	1.00 (0.067) mm.
r	0.8478	0.7898
a (var. a)	0.4708 (0.002396)	0.316 (0.00117)

A "t" test shows *S. cf. asteroidea* to have a significantly longer interarea ($0.02 > P > 0.01$). Although tests for allometric growth proved negative, it is apparent from a plot of the points on a graph (Text-fig. 2) that the specimens over 5 mm. long all tend to have relatively long interareas. These are all *S. cf. asteroidea* and thus may be biasing the "a" value.

Accordingly percentage values of length of interarea : length of valve (*m*) were calculated for the whole sample of *S. paucicostatus*, and compared with values of *S. cf. asteroidea* for a sample in the same size range, i.e. up to 4.9 mm. in length :

	n	.	.	.	<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
					19	34
\bar{m} (var. m)	37.4% (53.7)	33.6% (29.4)

On testing, $P \approx 0.06$, showing that with this selected sample the relatively greater interarea length of *S. cf. asteroidea*, just moves out of the 5% significance level.

For the ventral interior, a bivariate analysis carried out on the length of the spondylium (*s*) and the valve length (*v*) reveals no significant difference between the two samples :—

	n	.	.	.	<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
					16	11
v (var. v)	4.34 (2.091) mm.	3.13 (0.45) mm.
s (var. s)	1.53 (0.324) mm.	1.02 (0.078) mm.
r	0.8908	0.7764
a (var. a)	0.3937 (0.003394)	0.4163 (0.007649)

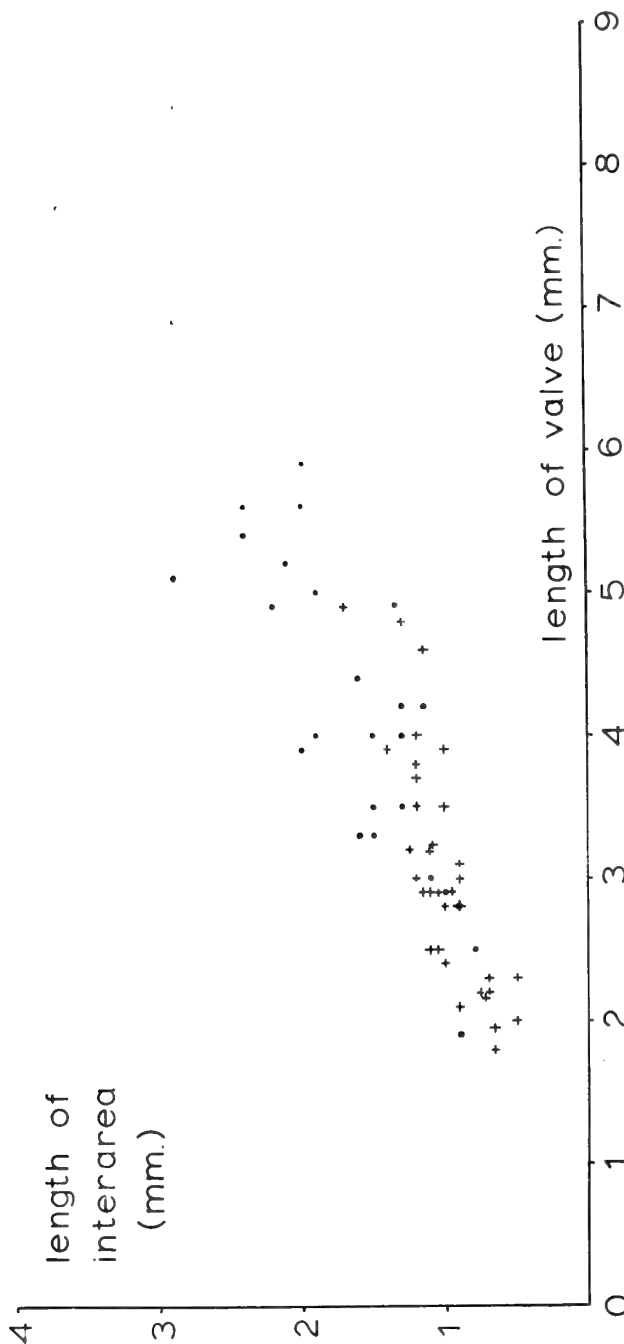


FIG. 2. Graph showing the relationship between the length of the ventral valve and the length of the ventral interarea in samples of *Skenidioides* cf. *asteroida* (Reed) (·), and *Skenidioides paucicostatus* sp. nov., (+).

As for the ventral valve, the dorsal outline for *S. paucicostatus* is significantly wider than for *S. cf. asteroidea*, 10 valves of the former having a mean percentage length : width of 51.2% (var. 65.7) compared with 65.7% (var. 86.6) for 15 valves of the latter ($P < .001$).

The length of the cardinalia : length of dorsal valve expressed as a percentage for 7 valves of *S. paucicostatus* are 27, 27, 30, 30, 31, 32, 33% ; and for 10 specimens of *S. cf. asteroidea* 22, 26, 26, 29, 30, 32, 32, 35, 37, 40% : these are not significantly different.

A bivariate analysis of the length of the dorsal median septum (s) : length of the dorsal valve (v) also shows no significant difference.

		<i>S. cf. asteroidea</i>	<i>S. paucicostatus</i>
n	.	15	11
\bar{s} (var. s)	.	2.89 (0.877) mm.	2.02 (0.225) mm.
\bar{v} (var. v)	.	3.89 (1.465) mm.	2.77 (0.295) mm.
r	.	0.8978	0.8112
a (var. a)	.	1.292 (0.02492)	1.145 (0.04982)

It is necessary to enlarge upon some details of the ornamentation given in the diagnosis, for this is one of the most important specific characters of the genus. The total number of ribs measured at 2 mm. from the ventral umbo for *S. cf. asteroidea* was 11–19 on 1, 4, 4, 4, 3, 2, 6, 1, 1 valves respectively ; and for *S. paucicostatus*, 7–13 on 5, 4, 8, 5, 2, 0, 2 valves respectively. A 2×2 test (Table 6) shows a significant difference in the two samples ($P < .001$).

TABLE 6

	7–11 ribs	12–20 ribs
<i>S. cf. asteroidea</i>	1	25
<i>S. paucicostatus</i>	24	2

TABLE 6. Table for 2×2 contingency test comparing the frequencies of ribbing densities for *S. cf. asteroidea* and *S. paucicostatus*, counts being taken at 2 mm. from the ventral umbo. At a distance of 3 mm. from the ventral umbo 12–21 ribs were present on 1, 2, 3, 2, 1, 1, 3, 0, 1, 1 valves of *S. cf. asteroidea* compared with 7–10 ribs on 2, 1, 3, 3 valves of *S. paucicostatus*.

While the mean wavelength of the ventral median costa of *S. paucicostatus* is significantly larger ($P < .001$) than its neighbouring lateral rib (0.77 mm. (var. 0.0203) and 0.48 mm. (var. 0.0051) respectively for 32 valves), the median and lateral ribs of *S. cf. asteroidea* show no significant difference (0.35 mm. (var. 0.0132) and 0.34 mm. (var. 0.0052) respectively for 24 valves) ; the lateral ribs of the former species are further significantly larger than those in the latter ($P < .001$).

The median rib of *S. paucicostatus* is invariably prominent. In *S. cf. asteroidea* the usually even ribbing is somewhat variable. Thus a median rib more marked than its neighbours was observed in 11/44 valves ; but in six of these the exaggeration was only very slight whilst in four of the other five valves it was due to the median rib producing a fascicle of ribs.

Skenidioides paucicostatus is quite distinct from all other described stocks of the genus, especially in the alate outline, the relatively few coarse ribs, and the strongly

developed median costa of the ventral valve. A stronger median rib also characterises the ventral valve of *S. mediocostatus* Cooper 1956, but is much less developed, measurements on Cooper's figures 19, 26 on pl. 97, c, giving a wavelength at 2 mm. of 0.5 and 0.4 mm. Further, the ribs as a whole are finer and more numerous (20, 19, 20 at 2 mm. on the three dorsal valves [figs. 21, 24 and 28]) than in *S. paucicostatus*. These two differences also apply to *S. costatus*. *S. oelandicus* (Wiman) from the Swedish Leptaena Limestone resembles *S. paucicostatus* in the alate hinge-line and other features, but possesses many more ribs and lacks the pronounced median rib of the ventral valve.

The second Portrane species is placed close to *S. asteroidea* (Reed). An examination of the type material of this species from the Drummuck beds at Girvan reveals close agreement with the Portrane valves particularly in shape and outline. The ornamentation is even and of the same style, with $2a^\circ$ developed before the other externals in the ventral valve. The ribbing is rather fine on the Scottish shells; but nevertheless both the wavelength and the total number of ribs are within the limits of variation of the Portrane material. Although Reed (1917 : 921) described the Drummuck specimens as having a less carinate and more rounded ventral valve than *S. craigensis*, one of the specimens of the type material (B.72689) certainly has a sharper and more angular fold than is usual in the Portrane shells, which tend to resemble the more gently folded specimen B.72691. Thus, while it seems certain that the Portrane shells are close to the Drummuck shells, a larger sample of the latter will have to be examined in order to ascertain whether the two are absolutely conspecific. *S. asteroidea* was recorded from both the upper and lower Drummuck by Lamont (1935 : 299). In the older Whitehouse Beds the genus is represented by *S. greenhoughi*, which has a finer ornamentation than *S. asteroidea*, according to Reed (1917 : 921) consisting of "24-30 simple rounded equal closely placed low ribs". A small sample of this species revealed a somewhat larger range in rib density with 32, 22, and 19 ribs present on three ventral valves at 3 mm. from the umbo. Including Reed's figured specimen (1917, pl. 21, fig. 32) which has 29 ribs at 3 mm., the sample of four is significantly different ($P=0.004$ in a Rank Sum Test) from the ten specimens of *S. cf. asteroidea* which show the largest number of ribs at this distance (see above p. 216).

Figures given for *S. cf. costatus* from the Gelli-grîn Calcareous Ashes by Williams (1963 : 376) show that it resembles *S. cf. asteroidea* in many characters. Comparisons of the length : width and length : height of the ventral valve, and of the length of cardinalia : length of dorsal valve reveal no significant differences. The ornamentation, too, is similar in the ventral valve development of $2a^\circ$ before $1a^\circ$, $3a^\circ$ and $4a^\circ$, but differs in having a median rib stronger than the rest in this valve. In this respect it resembles *S. paucicostatus* (see above).

S. billingsi from the Rockland Formation in Quebec (Schuchert & Cooper 1932 : 72) and *S. impressus* from the younger Percé Formation (Cooper & Kindle 1936 : 353) are the closest of the American species to *S. cf. asteroidea*, but both differ in possessing a finer ornamentation, which is well outside the range of variation of the Portrane shells.

Family **SAUKRODICTYIDAE** nov.

DIAGNOSIS. Aberrant biconvex and sulcate orthaceids with distinctive ornamentation of costae and costellae developed within a honeycomb network. Interareas short ; delthyrium and notothyrium open. Ventral interior with teeth supported by short, strong dental lamellae. Dorsal interior with short, divergent brachio-phores, with supporting plates which converge to form notothyrial platform ; cardinal process simple ; fulcral plates absent.

Genus **SAUKRODICTYA** nov.

DIAGNOSIS. Ventri-biconvex shells of rather transverse outline ; strong median fold on ventral valve and corresponding deep sulcus on dorsal valve ; anterior commissure sulcate. Radial ornamentation of costae and costellae forming integral part of honeycomb meshwork covering surface. Ventral interarea curved, apsacline ; dorsal interarea short, anacline ; delthyrium and notothyrium open. Shell substance apparently impunctate.

Ventral interior with teeth supported by short, strong, receding dental lamellae. Muscle field imperfectly known. Dorsal interior with deep sockets, without fulcral plates and bounded medianly by short brachio-phores, whose supporting plates converge medianly to form notothyrial platform ; this projects medianly into elongatedly subquadrate adductor field. Diductors inserted on notothyrial platform on either side of cardinal process, which is a low simple ridge.

DISCUSSION. The assemblage of characters possessed by the new genus indicates it to be an aberrant orthoid. These characters are however so distinctive that the genus cannot be placed in any existing brachiopod family with confidence ; accordingly the new family Saukrodictyidae is proposed to accommodate the single genus.

Unfortunately the type, and so far the only, species of the genus is rare in the Portrane faunas, and the few specimens available are all damaged. However, they are sufficiently well preserved to establish the majority of the structural features, although there is some doubt about the structure of the cardinal process. This appears to consist of a very low simple ridge on the notothyrial floor. A small piece of siliceous material does form a prominence along this ridge but it is uncertain whether this is part of the cardinal process which has been broken, or whether it is a small piece of silica adhering to the valve in this position.

The exterior features which immediately distinguish the genus from all other stocks are firstly the ornamentation and secondly the overall shape, with the very strongly developed ventral fold and dorsal sulcus.

The ornamentation consists umbonally of costae ; with growth of the shell these diverge, and in the intercostal spaces there develops a series of tiny calcareous plates perpendicular to the surface of the shell. These are arranged to form a basic pattern of two rows of " pores " between adjacent costae, with a zig-zag series of plates

dividing the rows longitudinally. The "pores" in fact are not holes at all, but simply spaces between the plates which form the walls of the honeycomb meshwork (Pl. 7, fig. 29). Thus, although the ribs usually project to a slightly greater extent, the honeycomb itself stands out markedly from the surface of the valve. Costellae may arise by a thickening along the line of the zig-zag series of plates; subsequently a double series of "pores" will again develop between the costella and the adjacent costa when increased growth permits.

Although in detail the ornamentation of *Saukrodictya* is quite unlike that of any other described brachiopod, several forms are known to have a rather similar ornamentation, including such genera as *Eichwaldia*, *Porambonites*, *Punctolira* and *Linoporella*.

Eichwaldia, whose taxonomic position is uncertain, has a net-like ornamentation, although it lacks the radial ornamentation of that in *Saukrodictya*. Here the resemblance ceases, *Eichwaldia* being totally different from the new genus in all features of the hinge region and valve interiors.

Whilst the syntrophoids *Porambonites* and *Punctolira* possess a net-like type of ornamentation, it gives the effect of single rows of fine pores usually arranged radially between fine radial costellae, a somewhat different arrangement from that of *Saukrodictya*. As with all syntrophoids, the fold and sulcus are on the opposite valve to *Saukrodictya*, whilst the internal structures further separate them from the Portrane genus.

Linoporella shows similarities to *Saukrodictya* in several ways. The ornamentation is, however, much closer in detail to that of species of *Porambonites* (Schuchert & Cooper 1932, pl. 18, fig. 33). The plication, although also found on the ventral valve, is extremely gentle and bears no comparison in degree of development to that of *Saukrodictya*. *Linoporella* also lacks the wide hinge-line of the new genus.

Internally the ventral valve of *Linoporella* has the dental plates continued forward to bound a somewhat elongate muscle field, anterior to which is a pronounced median ridge; *Saukrodictya* on the other hand has short receding dental plates and no median ridge. In the dorsal valve of *Saukrodictya*, the sockets are much deeper and the brachiophores less well developed than in *Linoporella*; this may be accounted for by the smaller size of the Portrane genus. Although *Saukrodictya* lacks the median septum and cruralium typical of the linoporellids, a certain similarity may be observed in the convergence of the brachiophore plates to form the notothyrial platform on the valve floor (instead of on a septum), and the muscle field too shows an elevated periphery as in some *Linoporella*.

The genus *Linoporella* is, of course, a punctate form. No evidence of punctation can be seen on the specimens of *Saukrodictya* but, as already indicated above (p. 168), in silicified material this is not necessarily conclusive. Should an unsilicified specimen be found in the other brachiopod faunas of the same age which are at present under investigation, and should this show the shell substance to be punctate, it will of course be necessary to transfer the family from the orthaceids to the dalmanellaceids.

TYPE SPECIES. *Saukrodictya hibernica* sp. nov.

***Saukrodictya hibernica* gen. et sp. nov.**

(Pl. 7, figs. 21, 23, 24, 26, 28-30)

DIAGNOSIS. Small, ventri-biconvex shells of transverse outline ; hinge-line wide, cardinal angles slightly obtuse, angular ; postero-lateral margin gently convex becoming strongly convex antero-laterally ; antero-medially the outline is affected by the strong fold. Ventral valve with prominent rounded fold giving trilobate appearance to valve ; dorsal valve with corresponding deep rounded sulcus, both fold and sulcus arising very close to umbones. Ventral valve with strong median costa along the fold, with about four costae developed on either side ; between costae, costellae develop within honeycomb meshwork. Ventral interarea curved, apsacline, about one-fifth as long as valve ; dorsal interarea very short, anacline ; delthyrium and notothyrium open.

Ventral interior with stout teeth supported by strong receding dental plates ; muscle field poorly defined by apparent marginal thickening showing scar to be rather broad, with median adductor scar extending slightly forward of diductor scars. Dorsal interior with short brachiophores, bounding deep sockets ; cardinal process ridge weakly developed, situated on notothyrial platform formed by convergence of brachiophore supporting plates ; notothyrial platform extended anteriorly into subquadrate adductor field from which it is clearly separated by raised periphery, produced from anterior continuance of brachiophore plates. Adductor field also with raised margin.

		Length	Width
HOLOTYPE.	Damaged dorsal valve		
	(BB.30255) . . .	3.1 mm.	—
PARATYPES.	Broken ventral valve		
	(BB.30256) . . .	4.1 mm.	—
	Broken ventral valve		
	(BB.30257) . . .	3.9 mm.	—

Superfamily **DALMANELLACEA** Schuchert & LeVene 1929

Family **DALMANELLIDAE** Schuchert & Le Vene, 1929

Genus **DALMANELLA** Hall & Clarke 1892

***Dalmanella portranensis* sp. nov.**

(Pl. 8, figs. 11, 12, 14-19, 21, 26)

- 1846 *Orthis testudinaria* Dalman ; M'Coy : 35.
 1853 *Orthis testudinaria* Dalman ; Medlicott : 268.
 1861 *Orthis testudinaria* Dalman ; Bailly : 12 (*pars*).
 1880 *Orthis testudinaria* Dalman ; Bailly : 82 (*pars*).
 1895 *Orthis testudinaria* Dalman ; Sollas : 101 (*pars*).
 1897 *Orthis elegantula* Dalman? ; Reed : 537.
 1897 *Orthis testudinaria* Dalman ; Reed : 537.
 1963 *Dalmanella* sp., Williams & Wright : 8.

DIAGNOSIS. Gently sulcate, ventri-biconvex shells of sub-circular outline. Ventral valves almost as long as wide, hinge-line about two-thirds of maximum

valve width ; thickness averaging about two-fifths of valve length. Lateral profile showing maximum convexity near umbo ; anterior profile with middle of valve more sharply convex than flanks, with only slight tendency to form a fold. Interarea curved, apsacline, approaching one-quarter as long as wide and one-sixth as long as valve ; delthyrium open. Dorsal valves over four-fifths as long as wide, and averaging about one-sixth as deep as long, shallowly convex in both profiles, anterior profile depressed medianly by narrow sulcus originating at umbo, becoming broad and shallow anteriorly to produce a gently and broadly sulcate anterior commissure. Interarea short, anacline, about one-eighth as long as wide ; notothyrium open. Ornamentation of costellae, typically with 3 ribs per mm. at 5 mm. anterior to dorsal beak.

Ventral interior with stout teeth, supported by strong dental lamellae which continue forward to define a muscle field averaging over two-thirds as wide as long and almost two-fifths as long as valve. Thickened adductor scar about one-third of the width of complete scar, and slightly shorter than bounding median diductor lobes. A pair of slightly divergent *vascula media* extend from anterior ends of median diductor lobes. Dorsal cardinalia extending for almost one-quarter of valve length comprising undifferentiated bilobed cardinal process with generally weak shaft on thickened notothyrial platform ; brachiophores subtending an angle of about 30° relative to plane normal to median ridge, and mean angle of divergence between posterior edges of brachiophores of about 60°, with angle of divergence of bases on valve floor slightly, but not significantly, less : socket pads, fulcral plates and crural pits variably developed. Subquadrate adductor field about two-thirds as wide as long and extending for half valve length, with anterior adductor pair larger and wider than posterior pair ; a weak median ridge divides the scar longitudinally.

		Length	Width
HOLOTYPE.	Dorsal valve (BB.30267)	10.1 mm.	10.8 mm.
PARATYPES.	Dorsal valve (BB.30268)	9.4 mm.	c. 11 mm.
	Ventral valve (BB.30269)	10.3 mm.	10.5 mm.
	Ventral valve (BB. 30270)	10.1 mm.	10.0 mm.
	Dorsal valve (BB.30271)	6.4 mm.	c. 7.5 mm.

DISCUSSION. This species of *Dalmanella* is of common occurrence in the Portrane Limestone, and has been recorded as *D. testudinaria* by various authors since 1846. *Dalmanella testudinaria*, also an Upper Ordovician form, has recently been redescribed from a sample of topotype material from Borenskult, Sweden (Williams & Wright 1963 : 29). A comparison of the data for the Swedish shells with the data for the Portrane shells (given below), shows that on external characters the two species cannot be distinguished.

Statistical tests on the outline of both dorsal and ventral valves reveal no significant differences in either the growth ratios or the initial shapes ; nor for the thickness : length ratio of the ventral valve. A bivariate analysis of thickness : length for the dorsal valve shows the value of the correlation coefficient, *r*, to be too low to warrant the determination of *a* and *b* ; but although the modal percentage for

the Swedish valves (14%) is less than for the Portrane specimens (17%), it still falls within the range (11–23%) for the Portrane sample.

The density of the ornamentation measured at 5 mm. anterior to the dorsal umbo shows 2–4 ribs present on 1, 27, 12 valves respectively, a very similar distribution to that of *D. testudinaria*. The more important rib relations are given in Table 7, the data for *D. testudinaria* being taken from Williams & Wright, Table 6. Of the larger counts obtained, only the relative development of 2a-1- to 2b- is markedly different in the two forms; but in view of the large number of specimens in which the earlier of the two ribs could not be determined, no significance can be attached to this difference.

TABLE 7

Relation	<i>D. testudinaria</i> s.s.	<i>D. portranensis</i>
1a-1- 1b- . .	3/5 (13) . .	0/2 (1)
2b-1- 2a° . .	4/5 (-) . .	- -
2c- 2a° . .	5/6 (-) . .	2/2 (-)
2b- 2a° . .	33/33 (-) . .	24/24 (-)
2a-1- 2b- . .	7/8 (24) . .	4/12 (12)
3c- 3a° . .	12/17 (1) . .	12/15 (3)
3b- 3a° . .	38/38 (1) . .	18/18 (3)
4b- 4b° . .	8/16 (13) . .	4/4 (-)
4a-1° 4b-1- . .	2/3 (3) . .	- -
3a-1-a- 2a° . .	28/28 (-) . .	16/17 (-)
3a-1-a- 3a° . .	- - . .	11/15 (2)
3b-1- 3c- . .	- - . .	0/10 (6)

TABLE 7. Table comparing the frequencies of twelve rib associations in the dorsal valves of *Dalmanella testudinaria* (Dalman) from Borensult, Sweden, with *Dalmanella portranensis* sp. nov. The number in parentheses indicates the frequency of valves in which the earlier rib of the association could not be determined.

In the dorsal valves, the tendency is for the cardinal process shaft and also the median ridge to be very much weaker in *D. portranensis* than in *D. testudinaria*, but this is not invariable. The statistical comparisons used for the brachiophores by Williams & Wright, i.e. the angle subtended by the brachiophores relative to a plane normal to the median ridge, the angle subtended between the posterior edges and also between the bases of the brachiophores, show no significant differences between these two species. For the first of these comparisons, a sample of 19 Portrane valves have a mean angle of 31.9° (var. 58.3); 37 valves show the mean divergence of the posterior edges to be 60.8° (var. 36.9), and the bases 58.5° (var. 43.4), the bases being slightly convergent but not significantly so.

The brachiophores of the Portrane valves do differ significantly from those of the Swedish shells in extending further forward relative to the length of the valves.

Length of cardinalia : valve length.

D. testudinaria, 5 valves—16, 19, 19, 20, 20%.

D. portranensis, 10 valves—18, 19, 21, 22, 22, 22, 23, 23, 25, 28%.

A Rank Sum Test carried out on these data indicates the two species to be significantly different ($P=0.020$).

The adductor scars have the same disposition in both species, with the maximum width located in the larger anterior pair ; although data for the Swedish shells is scant for both length : width of the scar, and for the length of the scar relative to the valve length, it does indicate the two species to be practically identical in both aspects.

Apart from the length of the brachiophores, the most striking difference between the two species is found in the ventral muscle field. The stronger dental lamellae of the Portrane species are almost subparallel in contrast to the weaker, widely divergent lamellae of the Swedish species ; the muscle field of the latter is accordingly broad and cordate in contrast to the narrower, subtriangular to slightly bilobate scar of the new species.

Rank Sum Tests on the dimensions of the muscle scar show the narrower scar of the Portrane species to be significantly different ($P=0.030$) from that of the Borenshult form, although there is no significant difference in the lengths of the muscle scar relative to the valve length.

Width : length of ventral muscle field.

D. testudinaria, 2 valves—80, 94%.

D. portranensis, 10 valves—67, 68, 68, 72, 73, 73, 74, 77, 79, 82%

Length of muscle field : length of ventral valve.

D. testudinaria, 3 valves—33, 36, 39%.

D. portranensis, 10 valves—35, 35, 35, 38, 38, 39, 40, 40, 40, 46%.

A ventral index (Williams & Wright 1963 : 18) of .45 was obtained for a solitary Portrane valve ; the lateral diductor lobe is situated on the lower part of the dental lamella and the adjustor scar in a well marked groove between the dorsal edge of the lateral diductor lobe and the tooth itself. Two valves show the median diductor lobes to extend beyond the adductor scar by 14 and 15% of their lengths ; and 4 valves possess an adductor scar whose width is 25, 25, 37, and 41% of that of the complete scar.

The species *Orthis wysogorskii* differs from *D. testudinaria* (and also *D. portranensis*) according to Wiman (1907 : 10), in having a ventral interarea which is almost in the plane of commissure and which is hardly curved (it may also be noted that it is very short, being less than 10% of the valve length in Wiman's pl. 1, fig. 23a), and also in the narrow angle of divergence of the brachiophores.

The closest of the Girvan shells of Upper Ordovician age to the new species are the Whitehouse form designated by Reed (1917 : 856) as *Dalmanella testudinaria* var. and the Drummuck *Dalmanella elegantula* var. *drummuckensis* (Reed 1917 : 850). Differences from the Portrane shells can be found in the posterior dorsal adductor scars being larger than the anterior pair in the former species, and in the short, broad ventral muscle scar (Reed 1917 : pl. 9, fig. 12) in the latter, which in spite of its poor definition anteriorly is closer to one-quarter of the valve length, rather than over one-third as in the Portrane species.

It becomes very evident from the work of Williams & Wright on the dalmanellids that details of the cardinalia and ventral muscle field in particular are fundamental in determining the *genus* to which dalmanellids belong ; and until an exhaustive study of the Whitehouse and Drummuck dalmanellids has been completed, comparisons with the Girvan shells will remain unsatisfactory.

The following statistical data were obtained for *Dalmanella portranensis*:—

Ventral valves.

Length (l) : width (w). $n=52$; \bar{l} (var. l) = 7.63 mm. (4.092) ; \bar{w} (var. w) = 8.01 mm. (4.270) ; $r=0.9795$; a (var. a) = 1.021 (0.0008472).

Length (l) : thickness (t). $n=53$; \bar{l} (var. l) = 7.95 mm. (4.185) ; \bar{t} (var. t) = 3.09 mm. (0.521) ; $r=0.9285$; a (var. a) = 0.3528 (0.000336).

Length (l) : width (w) of interarea. $n=26$; \bar{l} (var. l) = 1.21 mm. (0.09849) ; \bar{w} (var. w) = 5.20 mm. (1.724) ; $r=0.9042$; a (var. a) = 4.183 (0.1329).

Length of interarea (l) : valve length (v). $n=33$; \bar{l} (var. l) = 1.20 mm. (0.07406) ; \bar{v} (var. v) = 7.77 mm. (3.584) ; $r=0.8397$; a (var. a) = 6.956 (0.4603).

Width of hinge-line (x) : width of valve (y). $n=24$; \bar{x} (var. x) = 4.93 mm. (1.441) ; \bar{y} (var. y) = 7.58 mm. (3.922) ; $r=0.9326$; a (var. a) = 1.65 (0.01613).

Dorsal valves.

Length (l) : width (w). $n=32$; \bar{l} (var. l) = 8.17 mm. (2.686) ; \bar{w} (var. w) = 9.40 mm. (3.166) ; $r=0.9493$; a (var. a) = 1.086 (0.003886).

Length (l) : thickness (t). $n=19$; \bar{l} (var. l) = 8.51 mm. (1.994) ; \bar{t} (var. t) = 1.44 mm. (0.08638) ; $r=0.3581$.

Length : width of interarea, expressed as a percentage, 9 valves—10, 12, 12, 12, 12, 12, 14, 14, 15%.

Length : width of muscle field, 9 valves—57, 65, 65, 66, 67, 70, 70, 71, 72%.

Length of muscle field : length of valve, 6 valves—49, 51, 52, 53, 55, 57%.

Genus **BANCROFTINA** Sinclair 1946

***Bancroftina* sp.**

(Pl. 9, figs. 1, 2, 4, 5)

DESCRIPTION. Transverse dalmanellids with flatly convex dorsal valves, possessing a strong, rounded sulcus rising close to the umbo and becoming deep anteriorly ; sulcus bounded laterally by swollen flanks which flatten postero-laterally. Dorsal interarea short, slightly curved, strongly anacline, about three-quarters as wide as the valve ; notothyrium filled by myophore. Ornamentation costellate, with 3 ribs per mm. at 5 mm. antero-medial to the umbo.

Cardinal process with prominent, trilobed? myophore and weak shaft ; sockets bounded by brachiophores about one-sixth as long as the valve, with bases almost sub-parallel to hinge-line ; posterior edges of brachiophores diverge at 78°, bases at 97° in the figured specimen. Fulcral plates and crural pits absent, ancillary struts not well defined. Adductor field quadripartite, divided longitudinally by a strong rounded median ridge. Ventral valve unknown.

DISCUSSION. The above description is based principally on one fairly well preserved dorsal valve (BB.30272), 8.8 mm. long and 13.4 mm. wide, supplemented by a few other fragmentary dorsal valves. The cardinalia, comprising widely divergent brachioophores with the bases sub-parallel to the hinge-line without fulcral plates, together with a cardinal process which appears to be trilobed, suggest inclusion in *Bancroftina* rather than in any other dalmanellid genus. When compared with specimens of *B. typa* and *B. robusta* there are differences in detail ; the cardinal process of the Portrane specimens has a larger myophore which projects from the notothyrium, with a weaker shaft on a shallower notothyrial platform, and with the tops of the brachioophores rather more widely divergent than usual for the Caradocian forms. Externally the sulcus of the Portrane valves is certainly deeper than in the other species.

With the material available, the variation, particularly of the cardinalia, cannot be accurately assessed ; however, none of the differences observed in the Portrane material seem to be of more than specific importance, and the shells are accordingly placed provisionally in *Bancroftina*.

Family **SCHIZOPHORIIDAE** Schuchert 1929

Subfamily **ISORTHINAE** Schuchert & Cooper 1931

Genus **ISORTHIS** Kozłowski 1929

Isorthis ? **baillyi** sp. nov.

(Pl. 8, figs. 20, 22-25, 27-31)

DIAGNOSIS. Slightly asymmetrical ventri-biconvex shells of transversely oval outline, thickness of conjoined valves about three-fifths of ventral length ; anterior commissure rectimarginate. Ventral valves over four-fifths as long as wide, with maximum width at about mid-valve, hinge-line over half valve width ; interarea short, curved, apsacline, less than one-tenth of valve length ; delthyrium open. Lateral and anterior profiles evenly convex. Dorsal valve slightly shallower, evenly convex in lateral profile, with convex anterior profile very slightly indented medianly by short narrow sulcus, which is usually lost in valves over 4 mm. long ; interarea very short, anacline, notothyrium partially closed by cardinal process. Radial ornamentation of hollow angular costae and costellae, density 2 to 3 per mm. at 5 mm. growth stage ; branching dominantly internal.

Ventral interior with stout teeth, supported by dental plates which continue anteriorly as ridges to define muscle field, details of which are uncertain. Dorsal cardinalia composed of cardinal process with bilobed myophore and short, stout shaft, passing rapidly into shallow notothyrial platform ; brachioophore bases slightly divergent relative to tops in figured specimen, but not significantly so ; sockets defined by well developed fulcral plates. Subquadrate adductor field divided longitudinally by low median ridge, anterior adductor pair slightly larger than posterior pair.

		Maximum Length	Width
HOLOTYPE.	Complete shell (BB.30273)	8.5 mm.	9.7 mm.
PARATYPES.	Complete shell, ventral valve		
	slightly deformed (BB.30274)	6.5 mm.	7.9 mm.
	Dorsal valve (BB.30275)	6.4 mm.	7.5 mm.

DISCUSSION. This species is quite distinct from the associated *Dalmanella* in having a ventri-biconvex profile, an oval outline, a dorsal sulcus in the early growth stages which rapidly fades, a generally rectimarginate anterior commissure and a very short ventral interarea.

In profile and in the development of hollow costae especially, the Portrane species resembles Cooper's genus *Mendacella* (1930a : 377) which is known from Upper Ordovician as well as Lower Silurian strata. However, the disposition of the brachiophores of this stock is quite different, the bases being widely divergent relative to the tops (Williams & Wright, 1963 : 28) ; neither is the characteristic ventral sulcus developed in the Portrane valves, although this could be a reflection of the smaller size of the Irish shells.

The genus *Isorthis* has not, as yet, been recorded from the Ordovician or early Silurian rocks, and the Portrane species is placed here principally because of its greater morphological similarity to *Isorthis* than to any other described genus, the specimens not providing sufficient data for a categoric generic placing. The relatively coarse nature of the ornamentation is more characteristic of the associated *Dalmanella* than of known species of *Isorthis*, whose ornamentation is typically rather fine ; the attitude of the brachiophores, too, would appear to be intermediate between those of *Dalmanella* and of *Isorthis*, but with the large time interval involved the differences from *Isorthis* s.s. may not be as important as they first appear.

Using the Portrane sample at present available, the shells are placed provisionally with *Isorthis*. It may be that the species occurs elsewhere in rocks of similar age under the name of "*Dalmanella testudinaria*", a form from which it is certainly both specifically and generically distinct.

Family **DICOELOSIIDAE** Cloud 1948

Genus **DICOELOSIA** King 1850

Dicoelosia lata sp. nov.

(Pl. 9, figs. 3, 6, 9, 12, 14-19)

DIAGNOSIS. Transverse *Dicoelosia* with only moderate invagination of anterior margin producing characteristic bilobed appearance. Ventral valve about two-thirds as long as wide, with mid-line length four-fifths of maximum valve length, and two lobes diverging at average angle of 70°. Valve approaching half as deep as long, strongly and evenly convex in lateral profile ; anterior profile also strongly convex, grooved medianly by steep-sided narrow sulcus which originates at umbo and is less than 1 mm. wide at the 2 mm. growth stage. Interarea curved, apsacline, about one-quarter as long as wide and one-quarter as long as valve ; delthyrium

open. Hinge-line wide, about two-thirds of valve width ; cardinal extremities obtuse and flattened to produce small ears. Dorsal valve averaging three-fifths as long as wide, with uneven surface producing profile varying from gently convex to gently concave ; posterolateral areas flat, separated from median sulcus by strongly pronounced lobes, which themselves vary from convex to concave in lateral profile. Sulcus deep, originating at umbo, twice as wide as ventral sulcus and more gently rounded. Interarea very short, flat, anacline ; notothyrium open. Ornamentation of costae and costellae ; ventral valve with median costa in sulcus, which contains up to 8 ribs at front margin in largest specimens, with up to 13 in corresponding dorsal sulcus. Rib density of 4-6 ribs per mm. measured at 2 mm. distance antero-laterally along crest of lobe from ventral umbo. Dorsal ribbing pattern showing replacement of internal ribs by external ribs outwards from sector 2 to sector 4.

Ventral interior with teeth supported by convergent dental lamellae ; muscle field about as wide as long, and about one-third of valve length. Diductor scars extending slightly beyond but not enclosing median adductor scar. A pair of *vascula media* develop from anterior ends of diductor scars. Dorsal interior with long cardinal process ridge (shaft) on unthickened notothyrial floor, occasionally with small swelling (myophore) preserved at posterior end. Brachiphores blade-like, with bases slightly divergent on to valve floor to bound sockets ; cardinalia about half as long as wide, and about one-third as long as valve. Adductor scars and pallial markings not known.

		Maximum Length	Width
HOLOTYPE.	Complete shell (BB.30276)	. 4.5 mm.	5.6 mm.
PARATYPES.	Ventral valve (BB.30277)	. 4.6 mm.	7.0 mm.
	Ventral valve (BB.30278)	. 3.2 mm.	3.7 mm.
	Ventral valve (BB.30279)	. c. 3.6 mm.	5.3 mm.
	Ventral valve (BB.30280)	. c. 5 mm.	6.2 mm.
	Dorsal valve (BB.30281)	. 3.6 mm.	5.5 mm.
	Dorsal valve (BB.30282)	. 3.0 mm.	4.8 mm.

DISCUSSION. The genus *Dicoelosia* has a long stratigraphical range, being recorded from rocks of Upper Ordovician to Middle Devonian age. The Portrane form is characterised particularly by its transverse shape, wide hinge-line, the very moderate invagination of the anterior margin and the high angle of divergence of the two lobes. Detailed statistical data for these and other characters of the species are given below. For the bivariate analysis of maximum valve length to valve width of the ventral valves, a sample of 41 Portrane shells just failed to show allometric effects at the 5% level ($0.1 > P > 0.05$), whilst for a sample of 36 dorsal valves allometry was established ($0.05 > P > 0.02$). In his recent redescription of *Dicoelosia varica* (Conrad), Amsden (1958 : 53) includes data for 17 shells from the Haragan Formation of Oklahoma, which on testing show allometric effects for the outline of the ventral valve. Accordingly the corresponding allometric data for the Portrane shells are here included, and a comparison by "t" test of the length : width of the ventral valves shows the Irish form to be significantly more transverse ($0.01 > P > 0.001$)

than *D. varica*. This Devonian species is also quite different from *D. lata* in the convex dorsal valves and the relatively narrow hinge-line of the former, although the two are similar in the small degree of invagination of the anterior commissure. *D. oklahomensis*, from the Upper Silurian Henryhouse Formation, differs from *D. varica* in commonly having a more pronounced bilobation ; as evidence of this Amsden (1958 : 54) cites one specimen which has a median length : maximum length ratio of only 50%. Further data is not available for *D. oklahomensis*, but Amsden's earlier figures (1951, pl. 15) tend to confirm this deeper invagination, the median length being about 75 and 78% of the maximum length in his figures 5 and 7 respectively, which only just fall within the range for *D. varica* given in Table 3 (1958 : 53). Thus *D. oklahomensis* differs from the Portrane shells also on this character, as well as such features as valve outline and relative width of the hinge-line which it shares with *D. varica*.

The type species, *D. biloba* Linnaeus, is a Wenlock form whose exact range is still rather uncertain due to the rather indiscriminate use of this specific name in the past. The locality from which Linnaeus' type was obtained is not known (Davidson 1869 : 207) ; accordingly the attributes of the type species were obtained from Kozłowski's description of Polish shells placed in this species (1929 : 60). A comparison between this species and *D. lata* shows similarities in the valve convexities and in the anterior invagination, and differences in the less transverse outline, shorter hinge-line, and finer, less pronounced ribbing of the Wenlock form.

Amongst the described Ordovician stocks is *D. indenta* (Cooper) from the Whitehead Formation of Percé, Quebec. As stated by Whittard & Barker (1950 : 578), Cooper's figured specimen (1930, pl. 1, fig. 4) appears to be poorly preserved. They suggested that it may turn out to be identical with their Upper Llandovery form *D. alticavata*.

A sample of 46 Portrane ventral valves shows a mean divergence of the lobes (measured as the angle subtended by the ventral umbo and the antero-lateral extremities of the two lobes) of 68° (var. 64°) ; in Cooper's figure of *D. indenta* the lobes diverge at 53° , which is slightly less than the lowest recorded for the Portrane valves. In *D. alticavata*, the lobes diverge at "about $35\text{--}40^{\circ}$ " according to Whittard & Barker (1950 : 577) ; this agrees with their fig. 16 on pl. 8 (36°), although it is apparently somewhat higher (c. 52°) in fig. 18. Marked contrast between *D. lata* and these other two forms is further seen in their very deep anterior invagination and less transverse outline.

Reed (1917 : 848) recorded a variety of *D. biloba* from the Whitehouse Beds at Girvan, which is distinctive in possessing a marked central rib in the ventral sulcus ; on shell shape, however, Reed's figure (1917, pl. 9, fig. 4) falls within the range of variation of the Portrane valves on the length : width ratio, angle of divergence of the lobes, and the depth of the anterior invagination, although this last is rather deep for the Portrane sample. Reed's dorsal valve (fig. 6) has a length : width ratio of 90%, which is well outside the range of the Portrane sample. The Llandovery ventral valves figured by Reed (1917, pl. 9, figs. 1, 2) as *D. biloba* are, as noted by Whittard & Barker, quite distinct from the type species and they may be at once

distinguished from the Portrane shells by the less divergent lobes and the less transverse outline.

Dicoelosia cor, described by Wiman (1907 : 9) from the Leptaena Limestone of Sweden, shows a resemblance to the Portrane species in its general shape and small anterior invagination, as does the Whitehouse form. Strong costae develop sporadically, and a median one is present on the figured ventral valve (Wiman 1907, pl. 1, fig. 12) as in the Scottish shells. The Swedish species differs from *D. lata* particularly in the dorsal interior. Here the brachiophores are extremely long, protruding ventrally, in contrast to the low, plate-like brachiophores of *D. lata*. The bases of the brachiophores are also less divergent, and show a continuation anteriorly in the form of a low ridge to form a clear boundary to the muscle field, which is unknown in the Irish shells. Externally, the ventral valve of *D. cor* appears to lack a sulcus ; and the invagination of the anterior commissure appears to be even less pronounced than in *D. lata*, although most of Wiman's figured specimens are fragmentary, so that statistical data cannot be obtained for this character. The high interarea of the ventral valve (Wiman's fig. 13) is greater than for any of the Portrane sample, but in the text (p. 9) Wiman states that this character is very variable, most only being half the height of this figured specimen. The width of the interarea : valve width varies from 82% for his fig. 13a down to 52% for fig. 14, the range for the Portrane shells (see below) being very much less (57-75%).

A detailed study of the variation of the features of the Scottish and Swedish shells is necessary before the relations between these three can be satisfactorily ascertained.

The following statistical data was obtained for the Portrane sample :—

(a) *Ventral valves.*

Maximum length (l) : maximum width (w). $n=41$; \bar{l} (var. l) = 3.09 mm. (0.4647) ; \bar{w} (var. w) = 4.49 mm. (1.3315) ; $r=0.8604$; a (var. a) = 1.692 (0.01907) ; $\log_e \bar{l}$ (var. $\log_e l$) = 1.1045 (0.0475) ; $\log_e \bar{w}$ (var. $\log_e w$) = 1.4699 (0.0640) ; $r_e=0.8616$; α (var. α) = 1.161 (0.008973).

Mid-line length (m) : maximum length (l). $n=35$; \bar{m} (var. m) = 2.53 mm. (0.3691) ; \bar{l} (var. l) = 3.17 mm. (0.5285) ; $r=0.9679$; a (var. a) = 1.196 (0.002743).

Maximum length (l) : thickness (t). $n=19$; \bar{l} (var. l) = 3.31 mm. (0.3827) ; \bar{t} (var. t) = 1.50 mm. (0.09945) ; $r=0.8628$; a (var. a) = 0.5097 (0.003906).

Length of ventral valve (l) ; thickness of complete shell (t). $n=10$; \bar{l} (var. l) = 3.04 mm. (0.4845) ; \bar{t} (var. t) = 1.77 mm. (0.2312) ; $r=0.8202$; a (var. a) = 0.6908 (0.01953).

Length (l) : width (w) of interarea. $n=12$; \bar{l} (var. l) = 0.87 mm. (0.0334) ; \bar{w} (var. w) = 3.32 mm. (0.90) ; $r=0.8780$; a (var. a) = 5.190 (0.6172).

Length of interarea (x) : maximum valve length (y). $n=15$; \bar{x} (var. x) = 0.88 mm. (0.2821) ; \bar{y} (var. y) = 3.39 mm. (0.6045) ; $r=0.8806$; a (var. a) = 4.629 (0.3701).

Maximum width of interarea (x) : maximum valve width (y). $n=20$; \bar{x} (var. x) = 3.22 mm. (0.8547) ; \bar{y} (var. y) = 4.89 mm. (1.692) ; $r=0.9618$; a (var. a) = 1.407 (0.08247).

Length (l) : width (w) of ventral muscle scar. $n=11$; \bar{l} (var. l) = 1.28 mm. (0.1012) ; \bar{w} (var. w) = 1.17 mm. (0.0632) ; $r=0.9128$; a (var. a) = 0.7903 (0.01158).

Length of ventral muscle scar : valve length. 3 specimens only :— muscle scar 34, 34, and 36% of the valve length.

Origin of ventral sulcus (M mm. from umbo). $n=13$; \bar{M} (var. M) = 0.34 mm (0.0175).

Width of ventral sulcus at 2 mm. growth stage (m). $n=23$; \bar{m} (var. m) = 0.94 mm. (0.03727).

(b) *Dorsal valve.*

Maximum length (l) : maximum width (w). $n=36$; \bar{l} (var. l) = 2.85 mm. (0.2408) ; \bar{w} (var. w) = 4.71 mm. (1.132) ; $r=0.7863$; $\log_e \bar{l}$ (var. $\log_e l$) = 1.0328 (0.0290) ; $\log_e \bar{w}$ (var. $\log_e w$) = 1.5248 (0.0498) ; $r_e=0.7947$; α (var. α) = 1.31 (0.01928).

Mid-line length (m) : maximum length (l). $n=28$; \bar{m} (var. m) = 2.47 mm. (0.1700) ; \bar{l} (var. l) = 2.99 mm. (0.2467) ; $r=0.9605$; a (var. a) = 1.204 (0.008031).

Length (l) : width (w) of cardinalia. $n=16$; \bar{l} (var. l) = 0.92 mm. (0.06468) ; \bar{w} (var. w) = 1.81 mm. (0.1166) ; $r=0.8368$; $\log_e \bar{l}$ (var. $\log_e l$) = 1.8797 (0.0738) ; $\log_e \bar{w}$ (var. $\log_e w$) = 0.5759 (0.0348) ; $r_e=0.8426$; α (var. α) = 0.6866 (0.01009).

Length of cardinalia (c) : maximum valve length (v). $n=11$; \bar{c} (var. c) = 0.90 mm. (0.0708) ; \bar{v} (var. v) = 2.82 mm. (0.296) ; $r=0.8256$; $\log_e \bar{c}$ (var. $\log_e c$) = 1.8526 (0.0840) ; $\log_e \bar{v}$ (var. $\log_e v$) = 1.0185 (0.0365) ; $r_e=0.8288$; α (var. α) = 0.6592 (0.01538).

Width of dorsal sulcus at 2 mm. growth stage (M). $n=18$; \bar{M} (var. M) = 2.05 mm. (0.112).

(c) *Ornamentation.*

Rib density, measured at 2 mm. distance along the crest of the ventral lobe antero-laterally to the umbo, of 4–6 ribs per mm. on 14, 20, and 2 valves respectively. Data on costellae development, and ribs present in the sulci given in Tables 8–10 below.

TABLE 8

Rib relation		Frequency			
2a ⁻) 2a ^o	5/5
3a ⁻) 2a ^o	10/10
3a ⁻) 3a ^o	26/28 (3)
3a ⁻) 4a ⁻	10/10
3a ⁻ 1 ⁻) 2a ^o	4/4
4a ⁻) 4a ^o	0/10 (1)

TABLE 8. Frequencies of relative costella development on dorsal valves of *Dicoelosia lata* sp. nov., figures in parentheses indicating that the ribs arose simultaneously.

TABLE 9

Maximum shell length (mm.)	Number of ribs in the ventral sulcus						
	2	3	4	5	6	7	8
0.0-0.9	-	-	-	-	-	-	-
1.0-1.9	-	-	-	-	-	-	-
2.0-2.9	-	1	2	3	-	-	-
3.0-3.9	1	-	1	-	2	1	-
4.0-4.9	-	-	-	2	1	-	1

TABLE 9. Table showing the number of ribs present in the ventral sulcus at the anterior commissure for given lengths of valves.

TABLE 10

Maximum shell length (mm.)	Number of ribs in dorsal sulcus		
	11	12	13
2.0-2.9	3	1	-
3.0-3.9	1	1	1

TABLE 10. Table showing the number of ribs present in the dorsal sulcus at the anterior commissure for given lengths of valves.

Family **HARKNESSELLIDAE** Bancroft 1928Genus **REUSHELLA** Bancroft 1928**Reuschella** sp.

(Pl. 9, figs. 7, 8, 10, 11, 13)

1861 *Orthis vespertilio* J. de C. Sowerby ; Baily : 11.1880 *Orthis vespertilio* J. de C. Sowerby ; Baily : 82.1895 *Orthis vespertilio* J. de C. Sowerby ; Sollas : 101.

DESCRIPTION. Biconvex shells of transversely subrectangular outline, attaining up to 40 mm. in width ; strongly developed ventral fold and dorsal sulcus arising at the umbones. Cardinal angles usually obtusely rounded, with maximum valve width slightly anterior to the wide hinge-line. Ventral valve unevenly convex, about one-third as deep as long, with a sharply angular median fold standing well above the more gently convex flanks. Interarea curved, apsacline, about one-eighth as long as wide ; delthyrium open. Dorsal valve moderately convex in lateral

profile ; anterior profile deeply incised by the strong sulcus ; interarea very short, less than half as long as that of the ventral valve ; notothyrium open. Radial ornament coarsely fascicostellate, with about 30 angular costae and costellae developed at the 5 mm. growth stage on the dorsal valve. At the 5 mm. growth stage two ventral valves show a density of 3 ribs per 2 mm. immediately external to sector 1.

Ventral interior with teeth supported by strong dental lamellae which are continued anteriorly to form a raised periphery to the muscle field. Muscle field suboval, with narrow, strongly impressed median adductor scars bounded laterally, but not enclosed, by the diductor scars ; a pair of *vascula media* extend anteriorly from the thickened inner margins of the submedian diductor lobes. Dorsal interior with a swollen cardinal process situated on a thickened notothyrial platform ; myophore crenulated, of trilobed appearance with the median lobe extending more posteriorly than the lateral lobes, all lobes fusing into a short shaft anteriorly. Sockets long, widely divergent, defined by strong fulcral plates ; brachiophores short, subtriangular blades with grooved inner surfaces and dorsal edges convergent on to the sides of the notothyrial platform posteriorly, to form relatively deep crural pits.

Figured Specimens	Length	Width
Broken dorsal valve (BB.30283) . . .	20.5 mm.	c. 36 mm.
Asymmetrical dorsal valve (BB.30284) . . .	13.4 mm.	—
Dorsal fragment (BB.30285) . . .	13.6 mm.	—
Broken ventral valve (BB.30286) . . .	—	—
Ventral fragment (BB.30287) . . .	—	—

DISCUSSION. Of the 15 fragments of this form available for study, preservation was such that the ribbing relations (Bancroft, 1928a : 191) were obtained for just one small dorsal valve, and even then only the ribs of sectors 1–3 could be established with certainty. Only the following four relationships used by Bancroft (1945 : 238) and Williams (1963 : 415) regarding the relative insertion of the costellae were obtained for this specimen : — $2a^{-1-}$) $2a^{\circ}$, $2b^{-}$) $2a^{\circ}$, $3a^{\circ}$) $3a^{-1-}$, $3a^{\circ}$) $3b^{-}$. This indicates the relatively late insertion of $2a^{\circ}$, and early insertion of $3a^{\circ}$, typical relationships for the genus (Bancroft 1945, table 9).

A count of 29 ribs developed at the 5 mm. growth stage on a dorsal valve was supplemented by counts of 14, 15 and 15 taken on three half valves, confirming the development of about 30 ribs by this stage. The width : length of the ventral muscle scar has a ratio of two-thirds for one specimen ; from the evidence of broken specimens, however, this ratio would seem to be rather variable. The length : width for the cardinalia for two specimens is 38 and 62% ; but again the sample is insufficient for any statistical comparison to be made with other forms.

Williams (1963 : 414), in discussing the two groups of Anglo-Welsh *Reuschella* of Bancroft (1945 : 239), concludes that only ribbing can be effectively used to separate the *R. bilobata* group from the *R. horderleyensis* group. The convex nature of the Portrane ventral valves, with the sharp median fold separated from the convex

flanks simply by a change in slope, without lateral folds, would seem to rule out close affinity with the *R. bilobata* group. Further the transverse shape and strong ventral fold show that it is distinct from Whittington's species *R. oblonga* (1938 : 252), but with the material at present available for the Portrane shells, comparison with other species is rather unsatisfactory. Most other described species are earlier forms of Caradocian age, although it seems likely from Twenhofel's figures (1928, pl. 16, figs. 21, 22) that *Dalmanella ruida* from the Ellis Bay formation of Anticosti Island belongs to this genus, as well as the forms from the Ashgillian of Keisley and Kildare, which have been recorded as *Orthis vespertilio* (Reed, 1897 : 69 ; Reynolds & Gardiner 1896 : 593) and are still masquerading under that name.

It is interesting to note that the crural pits of the later Portrane forms are still relatively deep in large shells. This would indicate that Bancroft's idea of a gradual filling up of the crural pits during evolution, which was supported by Havlíček (1950 : 82), is not invariably valid.

Family **LINOPORELLIDAE** Schuchert & Cooper 1931

Genus **LATICRURA** Cooper 1956

Laticrura erecta sp. nov.

(Pl. 10, figs. 17, 18 ; Pl. 11, figs. 16, 18-21)

DIAGNOSIS. Subcircular ventri-biconvex shells, hinge-line about two-thirds of maximum valve width ; anterior commissure gently sulcate. Ventral valve about four-fifths as long as wide and two-fifths as deep as long ; anterior profile strongly and evenly convex with only slight indication of a fold ; lateral profile evenly convex with high, curved, apsacline interarea almost one-third as long as wide and one-quarter as long as valve ; delthyrium narrow, open. Dorsal valve about nine-tenths as long as wide and one-quarter as deep as long, with maximum convexity at umbo in lateral profile ; anterior profile depressed medianly by shallow sulcus. Interarea curved, anacline, less than one-tenth of valve length, notothyrium open. Ornamentation of fine hollow costae and costellae, typically with 4 ribs per mm. medianly at both 5 and 7.5 mm. growth stages.

Ventral interior with teeth supported by subparallel dental lamellae, whose anterior continuance defines an elongatedly rectangular muscle field about half as wide as long and two-fifths as long as valve. Apical plate usually well-developed ; adductor scar somewhat broader than flanking median diductor lobes, which may extend slightly farther forward ; lateral diductor lobes situated on dental lamellae. Dorsal interior with weak, linear cardinal process on notothyrial floor which thickens anteriorly, and is bounded laterally by almost vertical brachiophore plates ; brachiophores broad, "S"-shaped in section, and up to two-fifths as long as valve ; ventral edges diverging at about 60°, inside edges at approaching 40°. Sockets defined by fulcral plates, distance between being about one-third of valve width. Sharp, narrow median ridge extending in front of notothyrial platform for about

two-thirds of valve length, which may be over 1 mm. in height. Adductor scars poorly defined, about one-half as wide as long, and about two-thirds as long as valve.

		Length	Width
HOLOTYPE.	Dorsal valve (BB.30288).	11.5 mm.	12.9 mm.
PARATYPES.	Broken dorsal valve (BB.30289)	9.9 mm.	—
	Dorsal valve (BB.30290).	10.6 mm.	c. 12 mm.
	Ventral fragment (BB.30291)		
	and broken ventral valve (BB.30292)	—	—

DISCUSSION. This genus, first described by Cooper (1956) from the Caradocian rocks of the Appalachians, is also known to occur in rocks of the same age at Girvan. Although a total of five species have previously been attributed to the genus (*L. pionodema* Cooper, *L. latibrachiata* Cooper, *L. heteropleura* Cooper, *L. magna* Cooper and *L. inconstans* (Reed)), it is possible that the first and last pairs may prove to be conspecific (Williams 1962 : 145–146). Further, *L. heteropleura* is separated from the other American species essentially on the “great development of swollen and hollow costellae on the exterior” (Cooper 1956 : 981); but this seems to be simply a matter of degree, as a swollen rib also occurs at intervals in *L. latibrachiata* (Cooper 1956 : pl. 144, fig. 13; pl. 145, fig. 14) and in the Portrane species. These swollen ribs correspond in position to a rather deeper than usual marginal vascular groove on the inside of the shell.

Although the Portrane shells are similar to these other species in their general appearance, they show slight but significant differences in certain features. The new species is characterized by the more erect brachiophore supporting plates; a shallowly convex dorsal valve with a gentle sulcus and a marked subcircular outline; and a typical rib density of 4 ribs per mm.

The length : thickness ratio in 3 Portrane dorsal valves is 24, 26 and 26%. Williams (1962 : 144) records the dorsal valve of *L. pionodema* as being nearly one-third as deep as long. However, although the Portrane valves are generally shallower, comparison with the original data of Williams (22, 24, 31, 32, 33, 33, 38, 39%) shows that the difference is not statistically significant at the 5% level.

A comparison of the length : width percentage for 4 Portrane dorsal valves (79, 90, 93, 95%) with Williams' data for the Scottish sample of *L. pionodema* (76, 77, 77, 78, 82, 83, 83, 87, 89%), shows the former to be significantly less transverse than the latter ($P=0.025$).

The two species also differ in the density of the ribbing. In the Portrane dorsal valves, counts were taken medianly at 5 and 7.5 mm. from the umbo, 3–5 ribs per mm. being present on 1, 7, 2 valves and 1, 5, 0 valves respectively. Williams' figures (p. 145) for the Scottish shells, of 4–7 ribs per mm. on 1, 5, 4, 3 valves respectively show that these valves have significantly finer ornament than the Portrane valves ($P<0.001$ in a 2×2 contingency test with the measurements taken at the 7.5 mm. growth stage, see Table 11).

TABLE II

	2-4 costellae per mm.	5-7 costellae per mm.
<i>L. pionodema</i>	I	12
<i>L. erecta</i>	8	2

TABLE II. Table for a 2×2 contingency test comparing the frequencies of ribbing density for a sample of *Laticrura pionodema* from Girvan (data after Williams, 1962), and of *Laticrura erecta* from Portrane.

As observed by Williams (1962 : 145), there is no important difference between the ribbing densities of *L. pionodema* and *L. latibrachiata*, and his figures for the latter (5 and 6 costellae per mm. on 4 and 2 specimens respectively) again show the ribbing to be significantly finer than in the Portrane sample. In the outline of the dorsal valve, too, *L. latibrachiata* is very much closer to *L. pionodema*; Williams' raw data for the length : width of 6 specimens of *L. latibrachiata* are 71, 75, 78, 83, 83, 86%, these figures being significantly less than those for the Portrane sample ($P=0.033$).

A resemblance to *L. latibrachiata* is seen in the presence of an apical plate rather than a callist in the ventral valves of *L. erecta*; but the importance of this difference is questionable (Williams, p. 145). In the broad, shallow nature of the dorsal sulcus, the Portrane valves show greater similarity to *L. pionodema*, whilst that of *L. latibrachiata* is apparently narrow; but sulcus development seems to be very variable within *Laticrura* populations, and accordingly must be used with discretion as a specific character.

Williams' raw data for the length : width of 4 specimens of *L. inconstans* (63, 64, 68, 70%) show this form also to be significantly more transverse than *L. erecta* ($P=0.014$). Unlike the Portrane shells, *L. inconstans* has a fascicostellate ornamentation; as regards the rib density, the only data available show that it is 3 ribs per mm., so that the significance of this apparently coarser ribbing cannot be ascertained statistically. *L. magna*, which may be conspecific with *L. inconstans*, also differs from the Portrane shell in its transverse shape and fascicostellate ribbing, although in rib density, "about 4 to the millimetre at the anterior margin of the holotype", it evidently resembles the Portrane species.

L. heteropleura, too, has a more transverse outline than *L. erecta*, the holotype and figured paratype (see Cooper 1956 : 981) having dorsal length : width ratios of 75, 74% respectively. As indicated above, swollen ribs are present in both species, although this development is not so pronounced in the Irish Form.

Other biometrical attributes obtained for the new species include an assessment of the angle of divergence of the ventral edges, and also the inside edges, of the brachiophores, a sample of 12 valves having a mean (with variance) of 61° (43°) and 38° (5°) respectively. For the ratio of the length of the dorsal interarea : valve length, 7 valves show a mean of 8.99% (var. 0.37). Data for a bivariate analysis of length of median septum (s) : length of dorsal valve (l) for 9 valves is:— \bar{s} (var. s) = 6.8 mm. (1.03); \bar{l} (var. l) = 9.5 mm. (1.79); $r=0.8264$; a (var. a) = 1.318 (0.07872).

The mean length : width of the ventral interarea for 7 valves is 29.4% (var. 7.0) ; 3 valves show its length relative to valve length to be 23, 27, 28%. The width : length of the muscle field in 4 valves is 44, 51, 52, 63% ; a single valve shows the length of the scar : valve length to be 39%.

Superfamily **CLITAMBONITACEA** Winchell & Schuchert 1895

Family **CLITAMBONITIDAE** Winchell & Schuchert 1895

Genus **VELLAMO** Öpik 1930

Vellamo sulculata sp. nov.

(Pl. 10, figs. 1, 2, 4, 5, 8, 9, 11, 12, 14)

DIAGNOSIS. Plano-convex to strongly ventri-biconvex shells, transverse, with maximum width usually along hinge-line giving an alate appearance. Ventral valve of variable pyramidal shape, usually asymmetrical with umbonal region twisted. Interarea catacline to procline, rarely apsacline, with flat, concave, convex or irregularly terraced profile, approaching half as long as wide. Delthyrium about one-third as wide as hinge-line, closed by convex deltidium with large, tear-shaped foramen whose length averages almost two-fifths of interarea length. Narrow sulcus present posteriorly, becoming ill-defined by the 5 mm. growth stage, thereafter shallow, flattened or lost, except for median embayment in anterior margin. Dorsal valve about three-fifths as long as wide, flat to gently convex in lateral profile ; concave umbonally, posterolaterally and in median sulcus which separates gently convex flanks to produce a medianly indented anterior profile. Interarea very short, anacline ; notothyrium closed by low, gently arched chilidium. Ornamentation of even costae and costellae, totalling about 30 and 40 at the 5 mm. and 10 mm. ventral growth stages respectively. Fine concentric growth lines occasionally visible.

Ventral interior with teeth supported by deep, gently curved spondylium simplex with narrow flattened median zone developed in 27 out of 30 specimens ; in a single valve this zone is divided longitudinally, each part being the seat of attachment of an adductor muscle. Septum of spondylium extending for over half valve length, with rarely developed subparallel groove on either side corresponding to position of *vascula media*. Dorsal valves with notothyrial cavity divided by cardinal process ; posterior surface of notothyrial platform with two muscle scars on either side of cardinal process, inner pair marking position of attachment of diductor muscles, outer pair accessory diductor, or possibly dorsal adjustor, muscles. Socket ridges widely divergent, about one-fifth as long as wide. Quadripartite adductor field about half as long as wide and slightly less than half as long as valve, anterior pair longer than posterior. Adductor field divided longitudinally by rounded median ridge, which forks anteriorly to bound anterior adductor scars ; anterior scar subdivided into larger median scar and smaller lateral scar by oblique ridge which rises to prominent node on anterolateral edge of scar.

		Commissural Length	Width
HOLOTYPE.	Ventral valve (BB.30292)	c. 14 mm.	20.7 mm.
PARATYPES.	Damaged ventral valve		
	(BB.30293)	c. 12 mm.	c. 15 mm.
	Ventral valve (BB.30294)	8.5 mm.	14.4 mm.
	Broken dorsal valve (BB.30295)	—	26.4 mm.
	Asymmetrical dorsal valve		
	(BB.30296)	c. 11.5 mm.	c. 18 mm.
	Damaged dorsal valve		
	(BB.30297)	c. 11 mm.	c. 17.5 mm.
	Dorsal fragment (BB.30298)	—	—

DISCUSSION. Like the majority of species of the genus, *V. sulculata* is asymmetrical to a greater or lesser degree. Many Portrane shells also possess a superimposed tectonic deformation which is often difficult to distinguish from the natural asymmetry of the species. Generally, however, the following features indicate tectonic deformation. Laterally compressed shells are usually elongate, with the ribs very close together and showing narrowly pinched instead of rounded crests; valves compressed longitudinally are broad, and tend to have a convex profile; whilst forms squashed obliquely often show ribs which are pinched on one side of the valve and rounded on the other.

Davidson (1868 : 269) commented on the wide variation in shell shape of the specimens which now belong to the genus *Vellamo*, and the lack of adequate consideration of this factor has resulted in the erection of a wealth of species, many of which appear to be simply population variants. Until samples of the thirty or more species can be obtained, and the variation of the different attributes assessed with a statistical control, the affinities of the Portrane form (and of any other sample) have to be evaluated on the evidence of one or two specimens or figures and an accompanying description. Whilst this approach may be satisfactory with the more conservative shells, *Vellamo* shows such large variation that the procedure is somewhat inadequate.

Only two species of the genus have previously been described from the British Isles. *Clitambonites shallochensis* (Davidson) emend. Reed, which was placed in synonymy with *Vellamo pyramidalis* (Pahlen) by Öpik (1930 : 213), differs from *V. sulculata* in the presence of a very deep sulcus in the ventral valve. "*Clitambonites adscendens*" was described by Davidson (1868 : 278) from the Berwyn Hills, figured by Reed (1917) from Girvan and listed by others, e.g. Groom & Lake (1908), Lamont (1935). As stated by Öpik (1930 : 213), the British specimens belong to the genus *Vellamo*, and as *C. adscendens* Pander is the type species of *Clitambonites*, the *C. adscendens* of Davidson must be a separate species. These specimens differ from *V. sulculata* in having a much shorter ventral interarea "about six times as high as long", a less transverse outline and no indication of a ventral sulcus. Davidson's later figures (1883, pl. 16, figs. 16-18) again show the rounded outline, and a dorsal interior with the posterior adductor scars longer than the anterior scars. Figure 17, however, shows a higher interarea, and has a narrow groove in the posterior

part of the ventral valve, as seen in *V. sulculata*; but this groove is continued along the deltidium in Davidson's figure, suggesting that the shell is deformed. Reed (1917: 916) added little to the description, his figures (pl. 21, figs. 12-18) again showing the more rounded outline of these valves compared with the Portrane specimens.

Öpik (1934) listed 20 species and 3 subspecies of *Vellamo*, one of the species (*symmetrica*) being erected on a single valve and another (*aenigma*) on only two valves. The closest species to the Portrane form are *V. wesenbergensis*, *V. silurica*, *V. oandoensis*, *V. emarginata* and *V. pyramidalis*.

Although the dorsal muscle scars of *V. wesenbergensis* are rather poorly preserved in Öpik's figures (1934, pl. 10), the lengths of the muscle scar to the shell lengths are, as near as can be judged, 35, 34 and 38%, showing a significant difference ($P=0.008$) when compared with the data for *V. sulculata* (given below) in a Rank Sum Test. The ventral valve lacks a sulcus, although one is shown in *V. cf. emarginata* figured by Schuchert & Cooper (1932, pl. 7, figs. 16, 29, 30, 32) which Öpik (1934: 110) placed with *V. wesenbergensis*. However, this specimen does not show the posterior deepening of the sulcus as in *V. sulculata*, and differs further in having an apsacline interarea and a dorsal valve which broadens anteriorly. The Estonian form occurs in the Rakvere Stage, whose base marks the base of the Upper Ordovician (Harju Series) in Estonia (Rõõmusoks 1960: 58).

V. silurica occurs at the top of the Harju Series in the Porkuni Stage (F11). Until recently, this stage has been regarded by many authors (e.g. Jaanusson 1944) as being of Silurian age, which accounts for Öpik's specific name. *V. silurica* resembles *V. sulculata* in its rather transverse outline, procline interarea, style of spondylium, but shows no sign of a ventral sulcus (1934, pl. 12, fig. 12). *V. oandoensis* (D111 Stage) differs in having the dorsal anterior and posterior scars of about equal length, and in having a slight ventral fold (Öpik, pl. 12, fig. 11b). Figure 12, however, appears to show a narrow groove on the posterior part of the valve.

Of the earlier forms, *V. emarginata*, whilst possessing a sulcus on both valves, has a comparatively elongate outline for the dorsal valve, and shows a deep median groove in the spondylium. *V. pyramidalis*, which is also supposedly characterized by a sulcus in both valves, appears to lack this in one of Öpik's figures (1930, pl. 19, fig. 226).

Amongst the American species, the Richmondian *V. diversa* (Shaler) from Anticosti is distinguished from *V. sulculata* in its consistently apsacline interarea and in the socket ridges, which diverge at 90°-100°, in contrast to *V. sulculata* where they are almost parallel to the hinge-line. *V. multistriata* (Foerste 1912: 131) is quite distinct from the Portrane form in the fine nature of its ornamentation.

V. altissima (Winchell & Schuchert) is differentiated from their species *Clitambonites diversa* (non Shaler) solely on the "exceeding elevation of the cardinal area of the ventral valve" (1895: 381). The single specimen figured by them (pl. 30, fig. 19) shows the length: width ratio for the interarea to be 73%; whilst this is 10% higher than any from Portrane the significance cannot be established statistically.

on the solitary specimen. The width of the delthyrium : width of hinge-line (42%) is the same (within limits of error) as the highest found in *V. sulculata* : this feature was used by Raymond (1921 : 28) to distinguish his species *V. reudemanni* from *V. altissima*.

V. trentonensis (Raymond) is the closest of the American forms to *V. sulculata*, although Raymond's definition (1921 : 27) is not particularly diagnostic of the species. Raymond cited *Clitambonites diversa* Winchell & Schuchert (1895, pl. 30, figs. 11-17) as belonging to his species together with the specimens figured by Hall & Clarke (1892, pl. 15A, figs. 1-4, 7, 8). Figures 7 and 8 of Hall & Clarke are in fact of the same specimen that Winchell & Schuchert figured for their variety *altissima* in pl. 30, figs. 18, 19, so that Raymond included the specimen with *V. trentonensis* when figured by Hall & Clarke, but not when figured by Winchell & Schuchert, at the same time giving a specific name to Winchell & Schuchert's variety on the following page.

V. trentonensis differs from *V. sulculata* in having a spondylium with a clearly marked flat median area extending anteriorly ; in having the anterior adductor scars shorter than the posterior scars in the dorsal valve ; and in the possession of a rather angular chilidium. The figures of Schuchert & Cooper (1932, pl. 7, fig. 18) and Cooper (1944, pl. 3, fig. 33) apparently contradict the last two points, and underline the necessity for statistical comparisons between samples of the various species in order that the most important factor of variation be put in correct perspective. The exteriors figured by Hall & Clarke and Winchell & Schuchert, show the presence of a sulcus in both valves, and although it is seemingly absent from the umbonal region of the ventral valve, the other features of this apparently very variable species indicate that it is close to *V. sulculata*.

The following statistical data were obtained for the Portrane sample which comprises over 150 valves, although the majority of these are fragmentary or else tectonically deformed. The ventral valves possess a strongly pyramidal profile, and accordingly measurements have been taken for both the surface length and the commissural length (see Text-fig. 1). The low values of the correlation coefficient in the data for shell shape reflect the large shape variation of this species.

(a) *Ventral valve.*

Orientation of the umbo. In a sample of 40 valves, the umbones are directed posteriorly, anteriorly and vertically in 21, 15 and 4 valves respectively.

Width of delthyrium (x) : width of hinge-line (y). $n=12$; \bar{x} (var. x)=5.76 mm. (0.82) ; \bar{y} (var. y)=17.28 mm. (12.42) ; $r=0.89$; a (var. a)=3.89 (0.31).

Length (l) : width (w) of interarea. $n=12$; \bar{l} (var. l)=8.46 mm. (3.57) ; \bar{w} (var. w)=18.44 mm. (8.47) ; $r=0.37$.

Commissural length (c) : valve width (w). $n=8$; \bar{c} (var. c)=10.35 mm. (2.84) ; \bar{w} (var. w)=17.33 mm. (16.15) ; $r=0.46$.

Surface length (s) : valve width (w). $n=8$; \bar{s} (var. s)=13.16 mm. (10.31) ; \bar{w} (var. w)=17.33 mm. (16.15) ; $r=0.42$.

Length of foramen (f) : length of interarea (l). $n=13$; \bar{f} (var. f) = 3.32 mm. (0.64) ; \bar{l} (var. l) = 8.95 mm. (4.23) ; $r=0.41$.

Distance anterior to umbo where sulcus melts into flanks (l) : width of sulcus at this point (w). $n=12$; \bar{l} (var. l) = 4.36 mm. (2.43) ; \bar{w} (var. w) = 1.51 mm. (0.34) ; $r=0.7223$; a (var. a) = 0.375 (0.0067).

Distance from anterior end of median septum to anterior margin (x) : surface length of valve (y). $n=6$; \bar{x} (var. x) = 5.63 mm. (3.63) ; \bar{y} (var. y) = 13.48 mm. (12.48) ; $\log_e x$ (var. $\log_e x$) = 1.67 (0.109) ; $\log_e y$ (var. $\log_e y$) = 2.57 (0.067) ; $r=0.9614$; $r_e=0.9589$; a (var. a) = 1.85 (0.065).

(b) *Dorsal valve.*

Length (l) : width (w). $n=7$; \bar{l} (var. l) = 11.07 mm. (5.12) ; \bar{w} (var. w) = 18.1 mm. (17.7) ; $r=0.599$.

Length of adductor field : length of valve, 7 specimens—42, 43, 44, 48, 48, 49, 51%.

Length of anterior scar : length of adductor field, 7 specimens—57, 66, 67, 69, 70, 73, 76%.

Length : width of muscle field, 4 specimens—49, 50, 51, 52%.

Distance from angle of "fork" of median ridge to anterior margin (x) : valve length (y). $n=9$; \bar{x} (var. x) = 4.77 mm. (3.09) ; \bar{y} (var. y) = 9.14 mm. (6.77) ; $\log_e x$ (var. $\log_e x$) = 1.499 (0.127) ; $\log_e y$ (var. $\log_e y$) = 2.174 (0.078) ; $r=0.9426$; $r_e=0.9320$; α (var. α) = 0.78 (0.0115).

Length (l) : width (w) of socket ridges. $n=12$; \bar{l} (var. l) = 1.72 mm. (0.225) ; \bar{w} (var. w) = 8.86 mm. (4.623) ; $r=0.772$; a (var. a) = 4.53 (0.827).

In this last analysis, "length" is measured from the base of the cardinal process on the notothyrial platform to the most anterior extension of the socket ridges ; whilst "width" is taken as the distance between the points on either side where the socket ridges show a decided "kink" (in some specimens they terminate here, in others they continue towards the lateral margins as low ridges).

(c) *Surface ornamentation.*

Total numbers of ribs at the 5 mm. growth stage on 6 ventral valves are 24, 28, 29, 29, 30, 32 and on 4 dorsal valves 30, 33, 34, 37. At the 10 mm. growth stage, 2 ventral valves possess 38, 39 ribs and 3 dorsal valves 42, 46, 47 ribs.

Rib density is given in Table 12 below.

TABLE 12

Ribs/median 2 mm.	3	4	5	6	3	4	5
at 5 mm.	—	3	15	4	—	7	8
at 7 mm.	—	16	3	—	1	7	6
at 10 mm.	6	8	1	—	6	5	—
	(a)				(b)		

TABLE 12. Rib frequency for (a) ventral and (b) dorsal valves of *Vellamo sulcata* sp. nov., at various growth stages.

***Vellamo* sp.**

(Pl. 10, figs. 6, 7)

One dorsal valve (BB.30299) of this genus is quite distinct from *Vellamo sulculata* sp. nov. in possessing a differentiated radial ornamentation. The strong median costa is separated by a weaker costa (rib 2) from a strong lateral costa (rib 3) on either side ; both 2 and 3 produce an internal costella (2a- and 3a-), so that at the margin the three strong ribs are separated from each other by three finer ribs. External to the strong lateral costae, this differentiation is lost.

Although the valve is partially caked with silica on its inner surface, and the median parts of the chilidium and cardinal process broken, the cardinalia quite clearly indicate that the specimen belongs to the genus *Vellamo*, in spite of the unusual external ornamentation. The flat valve is 3.0 mm. long and has a maximum width along the alate hinge-line of over 6 mm., the cardinal extremity being broken on one side. Nineteen ribs are present at the margin.

Family **KULLERVOIDAE** Öpik 1934Genus **KULLERVO** Öpik 1934***Kullervo complectens* (Wiman) *albida* (Reed)**

(Pl. 10, figs. 3, 10, 13, 15, 16, 19, 20)

1917. *Clitambonites complectens* (Wiman), var. *albida* Reed: 916, pl. 21, figs. 19, 20.

DESCRIPTION. Plano-convex to strongly ventri-biconvex shells with a pyramidal ventral valve of B-shaped outline with maximum width about half the commissural valve length (see Text-fig. 1) located along hinge-line ; posterolateral regions concave, bounded by convex flanks on either side of a well-defined sulcus which is about one-fifth as wide as the valve. Ventral surface flat to gently convex in lateral profile, commissural length about three-quarters of surface length. Ventral interarea usually somewhat curved, apsacline umbonally becoming flat and catacline, about half as long as wide, and almost as long as the commissural valve length. Delthyrium about one-third as wide as the hinge-line, closed by convex deltidium with a pedicle foramen usually large, occupying up to half the length of the delthyrium and possessing an asymmetrical calcareous lip which may project up to 3 mm. away from the surface of the interarea. Dorsal valve with minute but prominent convex umbo, variably alate with maximum valve width at hinge-line, length to width ratios of 42, 44 and 58% being recorded for 3 valves ; valve profile flat, with gently convex areas developing antero-laterally, separated by a shallow sulcus medianly and bounded by flatter or concave areas posterolaterally. Elevated concentric ridges prominent over whole shell surface, usually stronger than the radial ornament although the ribs bounding the sulcus show a greater prominence in 2/10 ventral valves. Frequency of concentric ridges per 2 mm. of valve length, measured medianly anterior to 3 mm. growth stage, is 4, 5, 5, 5, 6 in five ventral valves. Concentric ornamentation invariably dominant and often the sole marking on

posterolateral areas of both ventral and dorsal valves ; elsewhere well developed costae and costellae produce a reticulate pattern with the concentric ridges. Ventral sulcus delimited on either side by costa which is clearly much stronger than any other radial rib in 10/12 specimens ; the other two specimens have a neighbouring one or two external costae of similar strength. Number of radial ribs in sulcus (and on shell) varies according to strength of development, with 5-7 on clearly reticulate forms, whilst only 1-3 may be discernible where radial ornament is less prominent, when concentric ridges tend to develop eminences in positions where ribs are developed in the more reticulate forms. Counts of strong ribs (and where reticulation is well developed, only the stronger ribs of the pattern) on left flank external to rib bounding sulcus show 1-4 ribs on 1, 5, 4, 2 specimens respectively. Total ribs occurring on flank external to sulcus bounding rib at 3 mm. growth stage are 7-10 on 4, 4, 0, 1 valves respectively ; these numbers are however very much dependent on the clear definition of the ribs. Dorsal ornamentation similar, with shallow sulcus bounded by strong rib on either side and a further 2 or 3 strong ribs external to these.

Ventral interior with simple teeth, spondylium supported by median septum receding ventral to spondylium but advancing near valve floor to pass into median ridge, the latter being simply an internal representation of the sulcus. Hemisyrix present, with hemisyringal walls variably developed ; subspondylial septa clearly seen in one specimen, which has a complementary ridge on the valve floor on one side. Traces of vascular markings observed marginally. Dorsal cardinalia dominated by ponderous, widely divergent socket ridges approaching one-third as long as wide, with only a narrow space between their thick posterior ends ; 3 valves show no cardinal process in this space ; 2 valves have a simple process, and another shows a small process developing medianly and ventrally from the chilidium, whilst a further specimen possesses a piece of siliceous material between the socket ridges which may or may not be a cardinal process. Antero-medianly socket ridges separated by thick notothyrial platform, passing anteriorly into a usually well defined median ridge. Chilidium, or traces of it, usually visible ; traces of adductor scars seen on only one side of a single specimen, located between median ridge and socket ridge with apices directed postero-medianly, typical for genus.

Figured Specimens	Length*	Width
Ventral valve (BB.30330) . . .	5.9 mm.	c. 11 mm.
Ventral valve (BB.30331) . . .	4.5 mm.	5.2 mm.
Dorsal valve (BB.30332) . . .	2.9 mm.	c. 6 mm.

* Overall length in plane of commissure, including deltidium.

DISCUSSION. The ventral sulcus of this species is quite clearly developed, although inclined to be shallow, and may broaden gradually to produce a narrow sulcus, or alternatively very rapidly to produce a wide sulcus (see Reed 1917, pl. 21, figs. 19, 20). A sample of 5 valves shows the mean width of the sulcus relative to valve width to be 21.3% (var. 8.5). The mean ratio of the commissural length : valve width for 5 ventral valves is 49.4% (var. 31.7) ; for 7 valves the ratio of

commissural length : surface length is 72.8% (var. 118.9). Data obtained for the ventral interarea shows the mean length to be 47.9% of the width (var. 47.2) in a sample of 5 valves ; a mean length relative to commissural length of 98.6% (var. 299.8) for 6 valves ; and the mean width of delthyrium : width of interarea of 34.2% (var. 22.3) in a sample of 5 valves.

The extremely large variation in the shape of the ventral valve of this species becomes apparent from the figures given above, so that it may be difficult to separate different samples on this feature alone. A statistical comparison has been made between the species here described and the three specimens of *K. lacunata* figured by Öpik (1934, pl. 36), using the length : width percentage of the socket ridges of the dorsal valve as a statistic. The figures for the Portrane sample of 7 valves are 25, 25, 27, 29, 32, 32, 33%, and for *K. lacunata* 34, 39, 39%. A Rank Sum Test indicates that the two species are significantly different in this attribute ($P = .008$).

The spondylium of *Kullervo* is an interesting one ; Öpik (1934 : 28) described it as being a degenerate spondylium triplex, the form of spondylium found in *Estlandia*, etc. This is based on the presence of a pair of ridges situated under either side of the spondylium which lie along the undersurface and extend for the length of the spondylium, in a somewhat similar manner to the hemisyringal walls on the upper surface, but further away from the median line than those structures.

Whittington & Williams (1955 : 413) disagreed with Öpik as they found " indications of the rudimentary 'spondylial septa' " in one specimen only ; and from their absence in other specimens, particularly in immature forms, they suggested that the " septa " were the products of mantle deposition in late stages of growth, and were probably not homologous with the lateral septa of the true spondylium triplex.

In brachiopods with an undoubted spondylium triplex such as *Antigonambonites* and *Estlandia* the middle septum is short, particularly in the umbonal region, so that the spondylium is close to the valve floor (Öpik 1934, text-fig. 3).

Progonambonites shows lateral septa at the apex of the spondylium which pass forward as ridges under the spondylium, with counterparts on the valve floor (Öpik 1934 : 27, text-fig. 4). At this stage the median septum is higher and stronger and deposition of the lateral septa as continuous partitions ceases. The condition in *Kullervo* may be likened to a late stage in this degeneration of the lateral plates, resulting from the elevation of the spondylium well above the valve floor.

In the Portrane material many specimens are caked with silica, especially internally, so that only 5 specimens show a clear spondylium. One adult shows very well developed subspondylial septa ; in the other specimens, especially the two younger ones, the ridges are not so obvious, due principally to the fact that in early stages they lie very close to the edge of the spondylium, only becoming clear as the spondylium deepens. The best specimen also shows a well defined ridge on the floor of the valve on one side which would correspond to the ventral base of the degenerate septum of Öpik's interpretation.

Thus whilst Whittington & Williams are certainly correct in calling this structure a spondylium simplex, it does seem likely that it evolved from a spondylium triplex,

as suggested by Öpik, by a strengthening of the median septum and weakening, with subsequent atrophy, of the lateral septa.

When Öpik erected the genus *Kullervo*, he used surface sculpture as a means of dividing the species into four groups (p. 162). In his first group he placed *K. panderi* Öpik and *K. intacta* Öpik, these being characterized by a dominant radial ornamentation, with a fine concentric ornamentation, and a reticulate pattern only on the ears (p. 165, fig. 37). The second group with *K. lacunata* Öpik and *K. aluverensis* Öpik shows strong radial ribs in the middle sector but on the ears the concentric ornamentation is dominant. In the third group *K. complectens* (Wiman) shows concentric ornamentation as strong as the radial over the whole of the valve; whilst *K. complectens albida* he placed in a fourth group with the concentric ornamentation dominant over the whole of the valve.

The strong concentric ornamentation of the Portrane species separates it from the first two groups. A species of *Kullervo*, *K. pyramidata*, was recorded by Cooper & Kindle (1936 : 353) from the Upper Ordovician Whitehead formation of Quebec. This is rather similar to the Portrane form (and *K. complectens*) especially in occasionally showing a distorted lip to the foramen. It differs from the Portrane form in having barely any sulcus in the ventral valve, radial ribs of even size and which seem to be much more prominent than the concentric ornamentation in the figures (Cooper & Kindle 1936, pl. 51, figs. 1, 2) although from the text the "heavy concentric lines (are) of almost as great strength as the costellae".

One other Irish species of *Kullervo*, *K. hibernica*, has been recorded by Harper (1952 : 100) from the Caradocian rocks of Grangegeeth. This is generally much closer to *K. panderi*, and differs from the Portrane specimens especially in its much finer and more even radial ornamentation.

Cooper (1956) has erected four species from the Lower Middle Ordovician of Virginia and Alabama. *K. ornata* differs from the Portrane species especially in the outline of the dorsal valve, being less transverse, without the alate hinge region, and lacking the concave posterolateral areas; and in possessing a very wide delthyrium (50% of the length of the hinge-line in his pl. 80, fig. 2), in the small apical deltidium and better developed walls to the hemisyrix. Cooper distinguishes this species from *K. parva* of the same horizon by the convex dorsal valve and subordinate concentric ornamentation of the latter. The ornamentation of *K. ornata* is much closer to the Portrane species than Cooper's other species in having the posterolateral areas covered dominantly by concentric ornamentation.

K. sulcata, known only from the ventral valve, resembles the Portrane form in having a well-defined sulcus bounded by a strong costella, but here, as in *K. parva*, the radial ornamentation is the dominant element in the middle sector of the valve. Cooper's other species, *K. punctata* differs considerably in shape and ornamentation from the Portrane form.

Reed (1917) erected his subspecies of *K. complectens* on two ventral valves from the Whitehouse Beds, Shalloch Mill, Girvan, stating it to differ from *K. complectens* s.s. only in having the radial ornamentation scarcely developed at all, so that the reticulate ornamentation is not so apparent (Reed, pl. 21, figs. 19, 20). Wiman's

form shows strong reticulation produced from radial and concentric ornamentation of equal strength (1907 : pl. 1, fig. 2b). In the Portrane sample four out of twelve ventral valves agree with Reed's types. Of the others one specimen shows a strong reticulation in the umbonal region only, whilst three other specimens showing this are small forms (i.e. may be compared to umbonal regions of large ones) of less than 4 mm. surface length. Two specimens show reticulation moderately developed, and only two with it well developed over most of the shell. So from this variation in the Portrane sample it would seem likely that a larger sample of the Girvan material may show this too.

The Portrane specimens are accordingly here placed in Reed's subspecies, differing from *K. complectens* s.s. in having the sulcus bounded by a rib stronger than the other ribs ; and in the concentric ornamentation being generally dominant, rather than equal to the radial ribbing.

Superfamily **TRIPLESIIACEA** Schuchert 1913

Family **TRIPLESIIDAE** Schuchert 1913

Genus **TRIPLESIA** Hall 1859

Triplesia* cf. *insularis (Eichwald)

(Pl. II, figs. 1, 2, 6, 7, 9, 10, 15)

- 1846 *Orthis galea* M'Coy : 30, pl. 3, fig. 12.
- 1853 *Orthis galea* M'Coy ; Medlicott : 268.
- 1861 *Orthis insularis* Eichwald ; Baily : 11.
- 1869 *Orthis insularis* Eichwald ; Davidson : 274, pl. 37, fig. 9.
- 1880 *Orthis insularis* Eichwald ; Baily : 82.
- 1895 *Orthis insularis* Eichwald ; Sollas : 102.
- 1897 *Triplesia insularis* (Eichwald) Reed : 537.
- 1963 *Triplesia* sp., Wright, pl. 109, figs. 13, 16-19.

DESCRIPTION. Large, dorsi-biconvex shells attaining over 25 mm. in width, lacking ornament except for occasional faint concentric growth lines. Ventral valve only moderately convex, transverse, with maximum width slightly posterior to mid-valve (valve length measured along line of lateral commissure). Sulcus, originating at about the 4 mm. growth stage, initially a curved depression ; later this flattens medianly and becomes more pronounced with the development of a long, evenly rounded and dorsally projecting tongue. Interarea curved, apsacline, about one-sixth as long as wide and two-thirds as wide as the valve ; delthyrium closed by flat pseudodeltidium, invariably with median fold ; beak perforated by pedicle foramen. Dorsal valve strongly globose, wider than long, with a low flat-topped or gently convex fold, slightly raised above the strongly convex flanks in anterior profile ; lateral profile convex, strongly so umbonally.

Tendency for umbonal thickening in the ventral interior, with slight development of pedicle passage, and pedicle tube in some valves ; teeth supported by weak dental lamellae, which diverge to limit the muscle field posterolaterally. Diductor scars large, flabellate, almost enclosing the cordate adductor field. Dorsal interior

with slender, forked cardinal process, whose width is only about one-quarter of the distance between the distal ends of the "brachioophores"; fork fused proximally into a single unit, hood invariably present; valve thickened umbonally.

Figured Specimens	Maximum Length	Width
Ventral valve (BB.30333)	22.5 mm.	c. 25 mm.
Damaged dorsal valve (BB.30334)	c. 21 mm.	c. 23 mm.
Dorsal fragments (BB.30335-36)	—	—

DISCUSSION. The etched specimens of this genus are poorly preserved, no dorsal valves and only 4 ventral valves being relatively complete. This is due in part to the normally very thin nature of the shells away from the umbonal regions, resulting in imperfectly silicified shells being easily damaged by the acid. A large number of the fragments consist simply of the dorsal hinge-line and cardinalia, the features of which have been recently discussed (Wright 1963 : 748). These are very distinctive when compared with those of the associated *Oxoplectra* (p. 248). The following statistical data were obtained for a sample of 14 specimens of the *Triplexia* in a bivariate analysis of cardinal process width (x) : distance between the tips of the brachioophores (y):— \bar{x} (var. x)=1.11 mm. (0.10); \bar{y} (var. y)=4.86 mm. (1.14); $r=0.796$; a (var. a)=3.3 (0.334).

The genus *Triplexia* is practically devoid of surface ornamentation, and as the internal structures are generally considered to be very conservative (e.g. the cardinalia) or else inadequately known for most species (e.g. pallial sinuses), specific differentiation is based principally on shell shape and the styles of folding. The species which show the greatest morphological resemblance to the Portrane specimens include *T. anticostiensis* Twenhofel 1914, *T. glabra* Williams 1951, *T. woodlandensis* Reed 1917, all of Llandovery age; and *T. uniplicata* Cooper & Kindle 1936, *T. asteroidea* Reed 1935, and *T. insularis* (Eichwald 1842), all of Upper Ordovician age.

Holtedahl (1916 : 87), in comparing the Oslo Llandoveryan *Triplexia* (*T. anticostiensis*) with the types of *T. insularis* from the Russian Lyckholm, pointed out that while there is much variation in form of the Norwegian shells, they differ consistently from the Lyckholm specimens in that the sulcus always arises at the umbo. Further the fold and sulcus are much more strongly developed in the Norwegian, and also the *Anticosti* forms, than in typical *T. insularis*. These are certainly more important characters than actual size and overall shape in any comparison of these two species, for whilst the Russian specimens which have been examined usually show a strongly galeate dorsal valve, this does vary, with some specimens being much more transverse in outline and proportionally less domed as in typical *T. anticostiensis*. The Portrane valves are accordingly separated from *T. anticostiensis* on the weak initial sulcus, and its comparatively late development in the Irish shells (originating in a sample of 7 valves at a mean distance of 3.54 mm. (var. 1.23) from the umbo). This feature also readily distinguishes the Portrane shells from *T. woodlandensis*, which has a very strong sulcus, arising at the umbo and which is sharply defined throughout its length.

T. glabra differs from the Portrane shells in having a well developed fold, which is ridged according to Williams' diagnosis (1951 : 104). With respect to *T. glabra*,

it may be noted that the median and lateral ridges are probably the result of abrasion of the shell, being a feature of the internal mould, not of the exterior. Pl. 11, fig. 15 shows within the thickened Portrane shell three ridges in the fold corresponding to a median groove and the grooves of the adductors on the valve interior. The outer shell layer is also partially preserved on this specimen and is quite smooth ; with the removal of this it is clear that the three ridges would be completely exposed, as is seen on the internal moulds of *T. glabra*.

T. uniplicata has a much narrower hinge-line than the Portrane shells, according to Cooper & Kindie (1936 : 358) the " (valve) width a little more than twice width of hinge ". Otherwise there seems little difference in the shape of the valves, and in fold and sulcus development.

The Drummuck species of Reed, *T. asteroidea*, is characterized by the presence of a pronounced groove extending along the length of the ventral sulcus (1935 : 7). This is absent from the Portrane shells, although certainly present in some of the specimens from the Chair of Kildare Limestone, where *T. biplicata* Cooper & Kindie and forms resembling *T. insularis* also occur at the same horizon. Future work on the Kildare *Triplexia* may show the three to be simply variants of the same species.

From the material available, the Portrane shells resemble *T. insularis* very closely ; the Irish specimens are, however, inclined to be rather transverse, but the significance of this cannot be ascertained until type material of *T. insularis* has been re-assessed and more complete specimens obtained from Portrane.

Genus **OXOPLECIA** Wilson 1913

Oxoplectia cf. ***plicata*** (Wiman 1907)

(Pl. 11, figs. 5, 8, 11-14, 17)

1846 *Spirifer terebratuliformis* M'Coy : 38, pl. 3, fig. 26.

1861 *Orthis biforata* Schlotheim ; Baily : 11 (*pars*).

1880 *Orthis biforata* Schlotheim ; Baily : 82 (*pars*).

1895 *Orthis biforata* Schlotheim ; Sollas : 102 (*pars*).

1897 *Orthis biforata* Schlotheim ; Reed : 537.

DESCRIPTION. Dorsi-biconvex shells, somewhat wider than long, with a hinge-line about two-thirds of maximum valve width, and a pronounced dorsal fold and ventral sulcus. Ventral valves about one-third as deep as long, evenly convex in lateral profile ; anterior profile with rather flattish flanks divided by median sulcus, originating at about 2.5 mm. from the umbo. Interarea curved, apsacline, about one-sixth as long as wide and about one-eighth as long as the valve ; delthyrium closed by flat pseudodeltidium, with median fold only occasionally developed. Foramen apical, anterior to delthyrium. Dorsal valve about three-fifths as deep as long, strongly convex with maximum convexity umbonally in lateral profile ; anterior profile with strongly convex flanks separated by a flat topped fold, originating at about 2 mm. from the umbo. Concentric ornamentation of growth lines,

about 5 per mm.; radial ornamentation of stout rounded costae, together with costellae produced by both bifurcation and implantation. Fold and sulcus initially with 3 and 2 costae respectively; on dorsal valve, wavelength of ribs at 7.5 mm. growth stage is about 1.3 mm., with total of 12-13 ribs developed at the 5 mm. growth stage.

Ventral interior with pedicle passage developed in the apex of a thick pseudodeltidium; teeth strong, supported by receding dental lamellae. Muscle scars poorly preserved, a single valve showing a narrow elliptical adductor scar. Dorsal valve with cardinal process broad proximally, almost half the distance separating the tips of the posteriorly directed "brachiophores", and deeply cleft with each prong fused more with the adjacent brachiophore than with the other prong. Hood not developed, commonly replaced by small pit. Shell substance thick posteriorly adductor scars and arcuate *vascula myaria* usually visible.

Figured Specimens	Length	Width
Ventral valve (BB.30337)	9.2 mm.	10.9 mm.
Dorsal valve, broken anteriorly (BB.30338)	—	21.6 mm.
Also broken dorsal valves (BB.30339-41) and a ventral fragment (BB.30342)	—	—

DISCUSSION. The sample of *Oxoplecia* obtained from the Portrane Limestone gives good evidence of the sorted nature of these deposits, as it shows the two opposing valves to be present in unequal quantities. This is a typical feature of disarticulated shells in sorted deposits, more especially in the case of valves which have markedly contrasted shape (as in the *Oxoplecia*), when the opposing valves behave differently on being subjected to current action, resulting from their different hydrodynamic properties.

The ratio of ventral to dorsal valves is practically the same at both principal localities from which a total of over a hundred valves was obtained; at locality 1 the ventral valves formed 12.5% of the total, and at locality 2 they formed 14% of the total.

Although specimens of the genus are moderately abundant, they are almost invariably broken, to such a degree that sufficient data are not available for an analysis of shell shape. The most useful criteria for identification of the species are found in the nature of the ornamentation, and in the very distinctive cardinal process. This differs from that of *Oxoplecia multicostellata*, *Triplesia extans*, *Triplesia ortonii* and most members of the superfamily, in possessing a groove instead of a ridge at the proximal end of the cardinal process (cf. *Triplesia* cf. *insularis*, Pl. 11, fig. 9). The only other triplesiaceid known to have this type of cardinal process is *O. plicata* from the Leptaena Limestone of Sweden; it may, however be present in other forms as the precise details of the cardinal process are unknown for the majority of triplesiaceid species.

The development of 2 initial costae in the sulcus and 3 on the fold distinguishes the Portrane form from most *Oxoplecia* species except for *O. subborealis* (Davidson 1883) emend. Williams 1962; *O. platystrophoides* and *O. costata* Cooper 1930; *O. abnormis*,

O. gibbosa and *O. parva* Cooper 1956 ; *O. perfecta* Cooper & Kindle 1936, and *O. plicata* (Wiman 1907) *non* Cooper 1956.

Twenty-nine Portrane dorsal valves have a mean rib wavelength of 1.28 mm. (var. 0.175) at the 7.5 mm. growth stage ; a comparison with Williams' data for *O. subborealis* (1962 : 153) reveals no significant difference. However, the number of initial costae on the fold is variable in the Girvan forms, which show both bicostate and tricostate patterns. Williams' Craighead sample is closer to the Portrane shells in this feature than the Balclatchie sample, having a proportion of tricostate : bicostate shells of 6 : 4. A 2×2 test indicates that the difference from the Portrane proportion (53 : 1) is significant ($P=0.001$). A further difference in the rib pattern is that, unlike *O. subborealis*, costellae are developed from both the first and second costae away from the fold on all valves complete enough to show this feature (23 and 21 respectively), the costae being either external or internal. The concentric ornament is finer too, with a mode of 5 per mm. instead of 8 as on the Girvan shells.

In *O. platystrophoides*, the two initial costae of the sulcus branch at 3 mm. to produce 4 ribs by the 4 mm. growth stage, where the sulcus develops ; 3 is the maximum number to occur in any Portrane valve. Although Cooper (1930 : 278) did not indicate the number of specimens examined, he made it clear that, unlike the Portrane shells, there are 2 primary costae on the dorsal fold, with the possibility of a third intercalated between them. In the other Percé form, *O. costata*, the ribs do not arise at the umbo, but much later (at 0.6 mm. in Cooper's fig. 4 on pl. 2) as in *O. mutabilis* Whittington & Williams (1955 : 411). *O. costata* is also characterised by 4 ribs being present in the sulcus.

The narrowly and transversely elliptical outline of *O. abnormis* serves to differentiate it from any other Chazyan form (Cooper 1956 : 539), and this also applies in the case of the Portrane shells. According to Cooper (1956 : 543), *O. gibbosa* has either 3 or 4 ribs on the fold, but the three figured specimens (pl. 102, A) all show 4 at the 5 mm. growth stage. For a 2×2 test comparing the proportion of specimens bearing 3 ribs with those bearing 4 or more (0 : 3 and 52 : 9 for *O. gibbosa* and *O. cf. plicata* respectively) $P=0.053$, showing no significance with this sample. *O. gibbosa* may be distinguished from the Portrane shells by the smooth valve surface for the first 3 mm. of growth, and the poorly developed nature of the ribs on the flanks. *O. parva* differs from *O. cf. plicata* also in its smooth umbonal region ; in the subdued nature of the ribs and their common absence on parts of the shell ; in the late development of the fold and sulcus ; and probably also in a larger number of ribs on the flanks.

From the morphology of the exterior, *O. plicata* and *O. perfecta* are the most closely allied forms to the Portrane species ; the character of the cardinal process is not however known for *O. perfecta*. Slight variations in the ribbing are to be found, but good samples of both the Swedish and the Canadian shells need to be examined before their true systematic value can be assessed.

O. perfecta differs from the Swedish and Irish shells in possessing a strongly incurved ventral umbo. The ribs of the figured specimen of *O. perfecta* (Cooper &

Kindle, pl. 51, figs. 25-29) are less prominent than in *O. cf. plicata*, but this may be due in part to the preservation; the left flank of the dorsal valve has 10 ribs at the margin, 7 on the fold, ? on the right flank, the specimen being 16.3 mm. long. A Portrane dorsal valve of length 16.4 mm. has 8, 9 on the left and right flanks respectively, and 6 on the fold. The fold of the Percé shell shows 5 ribs at the 10 mm. growth stage; if this is the modal value for that species, it may prove to be significantly different to the Portrane shells whose mode is 3, although 5 ribs do occur (see below).

The Portrane shells resemble the Swedish *O. plicata* in the wide, proximally divided cardinal process, the absence of a cardinal process hood, and the general lack of a median fold on the pseudodeltidium. The ventral valve figured by Wiman (1907, pl. 2, fig. 14) has the umbo disposed in a similar manner, and a rib count of 7 on each flank and 2 in the sulcus as in the Portrane shells. The dorsal valve (pl. 2, fig. 13) shows a rib wavelength of 1.3 mm., but differs from the Portrane valves in having 7 and 9 ribs on the flanks and 6 on the fold at the 5 mm. growth stage, the total of 22 being well above the range of the Portrane shells. This difference between the dorsal and ventral valves figured by Wiman suggests that the variation in the Swedish shells may be much greater than in the Portrane shells. Until a sample of the Swedish shells is obtained this variation cannot be further assessed; but it is quite clear that the Portrane shells are very closely related to, if not conspecific with, *Oxoplecia plicata*.

The following statistical data is included:—

Origin of dorsal fold (m). $n=22$; \bar{m} (var. m) = 2.15 mm. (0.13).

Origin of ventral sulcus (m). $n=11$; \bar{m} (var. m) = 2.55 mm. (0.341).

Width of cardinal process (x) (measured along an imaginary line joining the tips of the brachiophores): distance between tips of brachiophores (y). $n=14$; \bar{x} (var. x) = 2.16 mm. (0.103); \bar{y} (var. y) = 4.86 mm. (0.71); $r=0.8112$; a (var. a) = 2.63 (0.197).

Concentric ornamentation. 4-7 growth lines per mm. on 2, 6, 3, 1 specimens respectively.

Radial ornamentation in the ventral sulcus. (a) 12/12 specimens show 2 initial costae; (b) at the 3 mm. growth stage, 2, 3 ribs occur on 10, 1 valves respectively; at 5 mm. on 7, 2 valves; and at 10 mm. on 2, 1 valves.

Radial ornamentation on dorsal fold. (a) 2, 3 initial costae shown by 1, 53 valves respectively; (b) at the 3 mm. growth stage, 3, 4, 5 ribs shown by 56, 5, 0 valves; at 5 mm., on 52, 7, 2 valves; and at 10 mm. on 14, 7, 2 valves.

Total ribs on dorsal valves at the 5 mm. growth stage; 11-16 ribs on 4, 5, 5, 2, 0, 2 valves.

Oxoplecia cooperi nom. nov.

1956. *Oxoplecia plicata* Cooper: 555, pl. 104, E, figs. 25-31.

The new name is erected to replace *Oxoplecia plicata* Cooper, which is pre-occupied by *Oxoplecia plicata* (Wiman 1907: 12, 13).

Genus ***STREPTIS*** Davidson 1881***Streptis monilifera*** (M'Coy)

(Pl. II, figs. 3, 4)

1846. *Producta monilifera* M'Coy : 25, pl. 3, fig. 3.

DESCRIPTION. Dorsi-biconvex, uniplicate shells, with a ventral valve slightly longer than wide, due to the sulcus extending anteriorly in the form of a tongue ; cardinal angles roundedly obtuse, with maximum shell width slightly anterior to the hinge-line. Sulcus strong, rather "U"-shaped in profile, originating at 2.5 mm. anterior to the umbo in the figured specimen. Ornamentation on this valve consisting of nine strong concentric lamellae (frill bases), with superimposed radial costellae. Frill bases with wavelength of 0.9 mm., measured in the sulcus medianly, anterior to the 3 mm. growth stage ; on the immediate flanks the wavelength for the same lamellae is only 0.5 mm., adjacent lamellae becoming closer when traced to the posterior margin. Dorsal valve strongly convex with a low median fold, complementary to the ventral sulcus, which originates at 2.2 mm. from the umbo in the figured specimen ; shell broken, but is apparently somewhat wider than long. This shell shows nine frill bases, five being developed at a distance of 3.1 mm. from the umbo, with a wavelength of 0.55 mm. measured medianly immediately posterior to this growth stage.

Interiors of both ventral and dorsal valves obscured by silica, except for the hinge region of the latter, which shows a small, forked cardinal process with a small hood developed ; parts of the "brachiophores" visible laterally.

DISCUSSION. This species is of rare occurrence in the Portrane Limestone, only one ventral (BB.30343), 7 mm. long and 6.7 mm. wide, and one dorsal valve (BB.30344) being recovered, together with a ventral fragment ; adhering silica prevents an examination of the interiors, except for the features along the dorsal hinge-line.

The ventral fragment is part of a sulcus whose posterior side must certainly be over 3 mm. from the umbo. The style of this sulcus is similar to that of the complete valve ; the wavelength of the frill bases is 0.8 mm. ; and 5 radial ribs are present in a 2 mm. length, measured at right angles to the direction of growth.

Sufficient data are available to show that these shells belong to the species *S. monilifera*, topotype material of which was recently redescribed biometrically by Wright (1960). The plication on the Portrane dorsal valve is clearly present at a distance of 2.5 mm. from the umbo ; just perceptible at 2.2 mm. (designated as the origin in the above description) ; but not seen at the 1.9 mm. frill base. Posterior to this, the valve is badly abraded, but it is quite certain from the degree of development of the plication at the 2.2 mm. stage that it is absent from earlier stages. In *S. altosinuata* Hortedahl, a Llandovery form which is close to *S. monilifera*, the plication is already well developed at the 2 mm. growth stage. The position of origin of the plication is in fact one of the specific differences between the two forms, being at 1.16 mm. (var. 0.043) for a sample of 40 *S. altosinuata*, and at 2.0 mm. (var. 0.065) for 24 *S. monilifera* (Wright 1960 : 269).

The wavelength of the frill bases on the Portrane dorsal valve also resembles that of the Kildare form. In the latter case the measurement was taken anterior to the 3 mm. growth stage; accordingly precise comparison is not possible as the shell of the Portrane valve is missing medianly anterior to the 3.1 mm. position. Posterior to this, however, the wavelength is 0.55 mm., which compares closely with the mean of 0.52 mm. obtained for the Kildare shells (Wright 1960 : 271), in spite of the slightly different position of measurement.

Although the development of five frill bases by the 3.1 mm. growth stage of the dorsal valve may occur in either *S. monilifera* or *S. altosinuata*, this is the modal number for the former, compared with a mode of seven for the latter (Wright, Tables 2 and 3).

The presence of five radial ribs in 2 mm. on the ventral fragment cannot be closely compared with the Kildare material as the exact position of the fragment relative to the umbo is not known and Wright's figures (Table 1B) are given for the dorsal valve only. However, these Kildare data show that the occurrence of 4-6 ribs is more typical of *S. monilifera* than *S. altosinuata*.

Thus the details of the ornamentation, together with the strong overall resemblance between the Portrane and Kildare shells (particularly in the dorsal valves, see Wright 1960, pl. 1, fig. 17), clearly indicate the two forms to be conspecific.

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PLATE 1

Orthambonites humilidorsatus sp. nov.

- FIGS. 1, 6, 7, 10. Ventral, dorsal, lateral and anterior views of complete shell. BB.30152. $\times 2.6$.
FIG. 2. Interior of broken dorsal valve showing cardinal process and remaining brachiophore. BB.30154. $\times 4.3$.
FIG. 3. Antero-dorsal view of ventral interior to show muscle field. BB.30155. $\times 3.1$.
FIGS. 4, 5. Lateral and exterior views of ventral valve. BB.30151. $\times 2.6$.
FIG. 8. Interior of incomplete dorsal valve showing cardinalia. BB.30153. $\times 4.4$.
FIG. 9. Interior of ventral fragment, showing muscle field. BB.30156. $\times 3.8$.
FIGS. 11, 12. Interior and exterior of ventral valve. Holotype, BB.30150. $\times 2.3$.

Taphrothis ? sp.

- FIGS. 13, 17. Exterior and interior of dorsal valve. BB.30158. $\times 1.7$.
FIGS. 14, 18. Exterior and interior of ventral fragment. BB.30159. $\times 1.8$.
FIGS. 15, 16. Exterior and interior of dorsal fragment. BB.30157. $\times 1.6$.
FIGS. 19, 20. Exterior of two ventral fragments, BB.30160 and BB.30161 respectively. $\times 1.7$.

Glyptorthis maritima sp. nov.

- FIG. 21. Interior of dorsal fragment showing muscle field. BB.30180. $\times 1.7$.
FIG. 22. Interior of damaged dorsal valve showing cardinalia. BB.30178. $\times 1.7$.
FIG. 23. Exterior of ventral valve. BB.30177. $\times 1.7$.
FIG. 24. Dorsal interior of young specimen. BB.30181. $\times 3.7$.
FIGS. 25, 26. Exterior and lateral views of ventral valve. BB.30176. $\times 1.7$.
FIG. 27. Interior of ventral fragment showing muscle field. BB.30179. $\times 1.7$.
FIGS. 28, 29. Exteriors of two dorsal valves ; BB.30175 $\times 1.6$; holotype, BB.30174 $\times 2.2$, respectively.

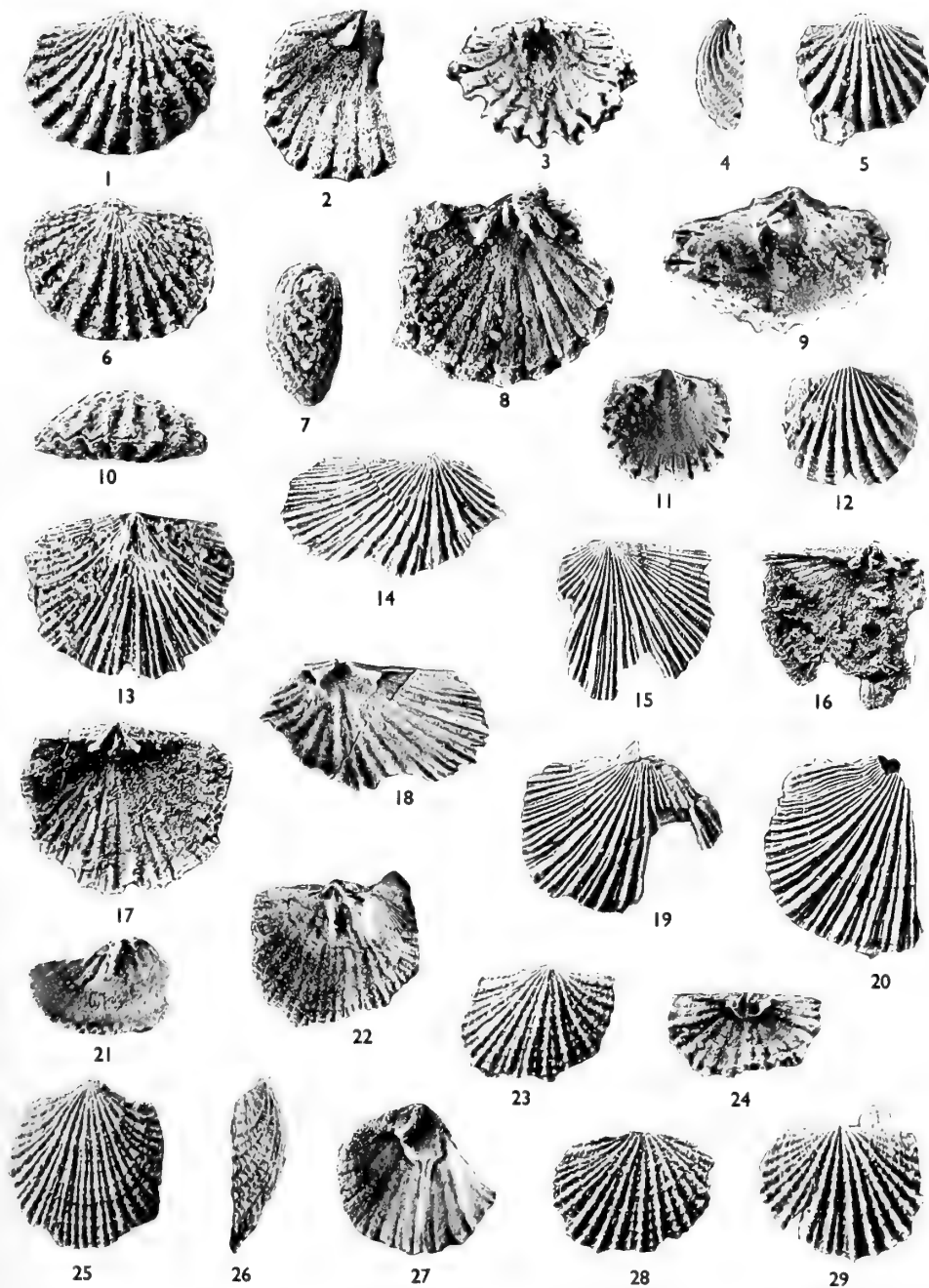


PLATE 2

Nicolella actoniae (J. de C. Sowerby)

- FIGS. 1, 2. Exterior and interior of ventral valve, broken anteriorly. BB.30163. $\times 1.7$.
FIG. 3. Dorsal exterior showing notothyrium filled by chilidial plates and cardinal process. BB.30164. $\times 1.7$.
FIG. 4. Dorsal interior showing cardinalia and muscle field. BB.30165. $\times 1.7$.
FIGS. 5, 6, 7, 11. Lateral, ventral, dorsal and anterior views of complete shell. BB.30162 $\times 1.7$.
FIG. 10. Fragment of ventral valve showing nature of interior at commissural margin. BB.30166. $\times 1.7$.

Hesperorthis sp.

- FIGS. 8, 9, 14. Lateral, exterior and interior views of ventral valve. BB.30172. $\times 1.7$.
FIG. 20. Dorsal interior. BB.30173. $\times 1.6$.

Portranella angulocostellata gen. et sp. nov.

- FIGS. 12, 13, 18. Exterior, and two interior views of dorsal valve to show cardinalia; specimen raised slightly at anterior end in Fig. 13. Holotype, BB.30167. $\times 2.7$.
FIGS. 15, 16. Exterior and interior of ventral valve. BB.30169. $\times 2.5$.
FIG. 17. Exterior of damaged dorsal valve. BB.30171. $\times 1.9$.
FIGS. 19, 22. Posterior and interior views of broken dorsal valve to show cardinalia. BB. 30170. $\times 3.1$.
FIG. 21. Interior of ventral valve, viewed antero-dorsally, to show pedicle callist. BB.30168. $\times 5.3$.

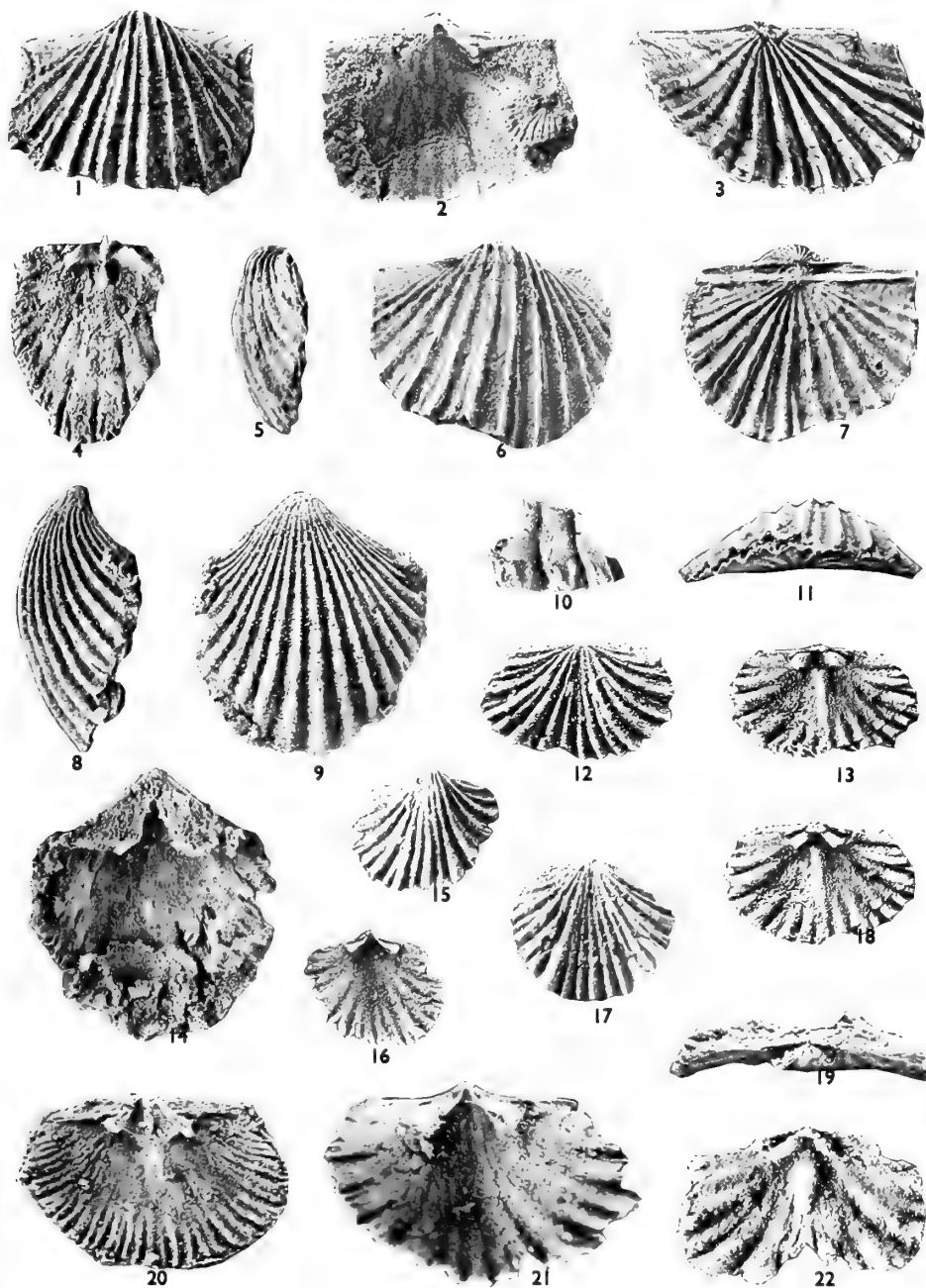


PLATE 3

Glyptorthis maritima magna subsp. nov.

- FIGS. 1, 2. Exterior and interior of incomplete ventral valve. BB.30183. $\times 1.2$.
FIGS. 3, 4. Exterior and interior of damaged ventral valve. BB.30184. $\times 1.7$.
FIG. 5. Interior of broken dorsal valve. BB. 30185. $\times 1.2$.
FIG. 6. Interior of dorsal valve showing well-preserved pallial markings. Holotype, BB.30182. $\times 1.6$.
FIG. 18. Exterior of broken dorsal valve. BB.30186. $\times 1.8$.

Ptychopleurella twenhofeli nom. nov.

- FIGS. 7, 8. Exterior and interior of dorsal valve. BB.30189. $\times 3.8$.
FIGS. 10, 11, 12, 19, 20. Lateral, ventral, dorsal, posterior and anterior views of complete shell. BB.30187. All $\times 3.8$, except Fig. 20, $\times 4.4$.
FIGS. 24, 28. Exterior and interior of ventral valve. BB.30188. $\times 3.8$.
FIG. 22. Enlargement of Fig. 28, to show muscle field and apical plate. BB.30188. $\times 5.5$.

Ptychopleurella separata sp. nov.

- FIGS. 9, 13, 15, 16. Posterior, ventral, anterior and lateral views of ventral valve. Holotype, BB.30190. $\times 4.0$, $\times 3.4$, $\times 3.8$, $\times 3.4$ respectively.
FIG. 14. Exterior of dorsal valve. BB.30191. $\times 3.3$.

Dolerorthis inaequicostata sp. nov.

- FIG. 17. Interior of ventral valve. BB.30212. $\times 1.9$.
FIGS. 21, 25. Interior and exterior of broken dorsal valve. BB.30214. $\times 1.8$.
FIG. 23. Exterior of dorsal valve. Holotype, BB.30210. $\times 1.8$.
FIG. 26. Exterior of ventral valve. BB.30211. $\times 1.7$.
FIG. 27. Interior of ventral valve. BB.30213. $\times 1.8$.

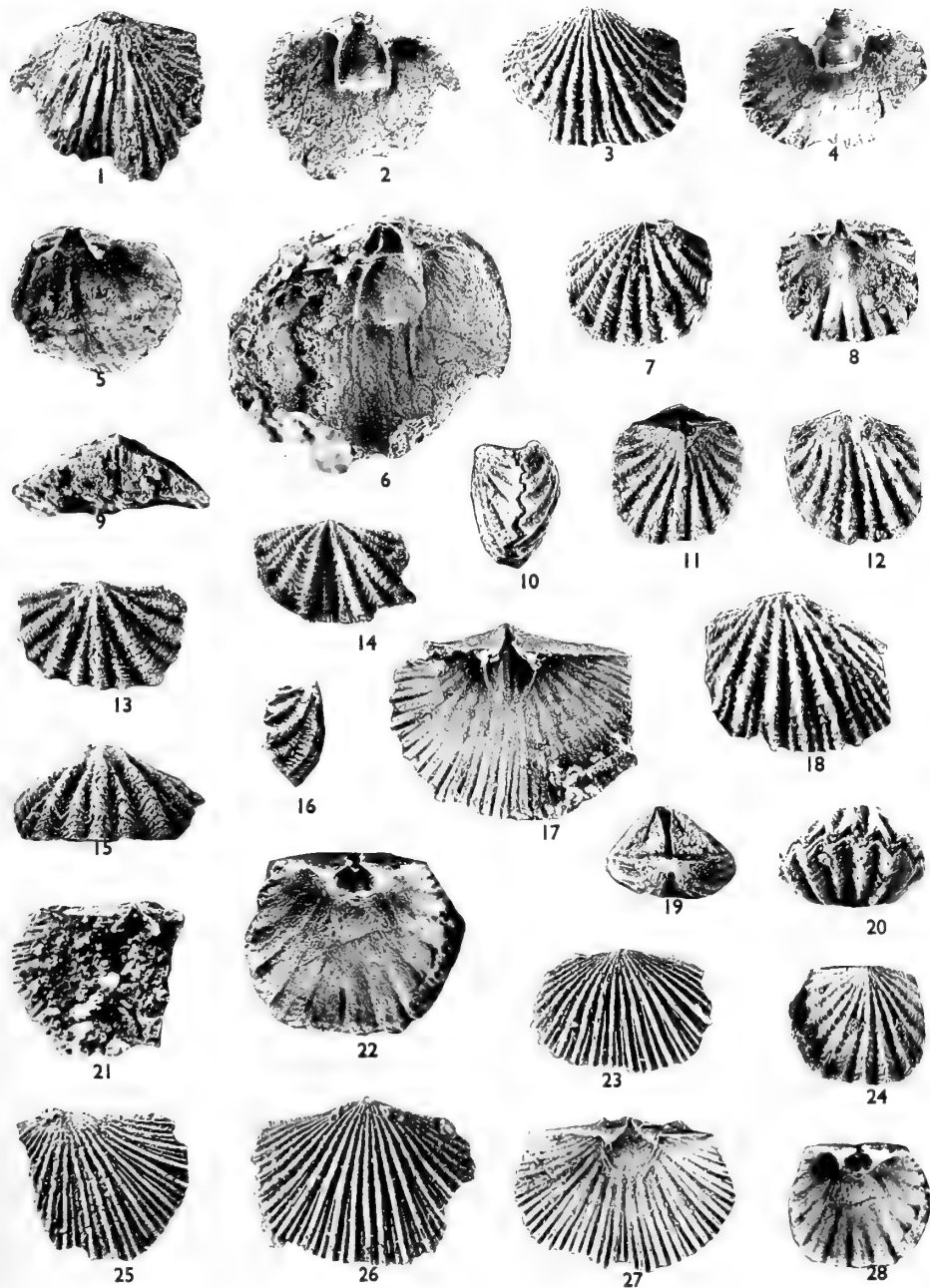


PLATE 4

Plaesiomys porcata (M'Coy)

FIG. 1. Exterior of ventral valve. BB.30199. $\times 1.5$.

FIGS. 2, 5, 6, 7. Four incomplete ventral valves showing variable outline and features of ventral muscle field ; pallial markings well shown in Fig. 2. BB.30202, BB.30203, BB.30204, BB.30205. $\times 1.1$, $\times 1.6$, $\times 1.6$, $\times 1.5$ respectively.

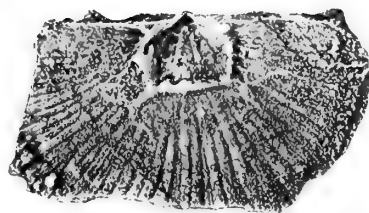
FIGS. 3, 4. External and lateral views of damaged dorsal valve. BB.30201. $\times 1.3$.

FIG. 8. Exterior of small ventral valve, broken anteriorly and with procline interarea. BB. 30200. $\times 1.5$.

FIGS. 9-12. Four fragmentary dorsal valves showing cardinalia and usually lightly impressed adductor muscle field. BB.30206-09. $\times 1.7$, $\times 1.6$, $\times 1.5$, $\times 1.6$ respectively.



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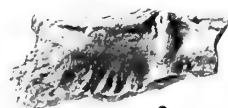
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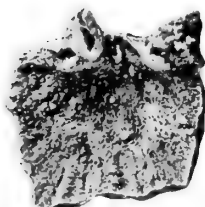
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PLATE 5

Spinorthis geniculata gen. et sp. nov.

FIGS. 1-3. Exterior, interior and lateral views of ventral valve. Holotype, BB.30192. $\times 2.1$.

FIG. 4. Exterior of dorsal valve. BB.30193. $\times 2.2$.

FIGS. 5, 6. Interior and exterior of dorsal valve. BB.30194. $\times 2.1$.

FIGS. 7, 8. Exterior and interior of ventral valve. BB.30195. $\times 2.3$.

FIG. 10. Fragment of dorsal valve, showing well developed spines. BB.30198. $\times 3.5$.

FIG. 11. Interior of broken ventral valve. BB.30196. $\times 2.5$.

FIG. 12. Exterior of small, damaged, dorsal valve. BB.30197. $\times 4.0$.

Schizophorella fallax (Salter) *silicis* subsp. nov.

FIG. 9. Interior of damaged ventral valve. BB.30230. $\times 1.4$.

FIGS. 13-16. Interior ($\times 1.5$), exterior, lateral and anterior views ($\times 1.3$) of ventral valve. BB.30226.

FIG. 17. Interior of broken dorsal valve. BB.30227. $\times 1.5$.

FIGS. 18, 19. Exterior and lateral views of ventral valve. Holotype, BB.30224. $\times 1.5$, $\times 1.3$ respectively.

FIGS. 22, 23. Two broken ventral valves showing strongly developed muscle fields. BB.30228-29 respectively, $\times 1.4$.

Plectorthis sp.

FIGS. 20, 21. Interior and exterior of broken dorsal valve. BB. 30221. $\times 1.6$.

Hebertella sp.

FIGS. 24, 25. Interior and exterior of damaged ventral valve. BB.30222. $\times 2.0$.



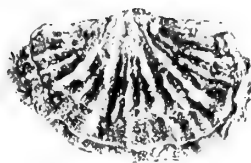
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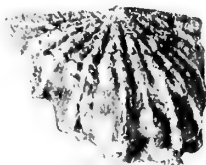
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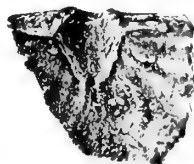
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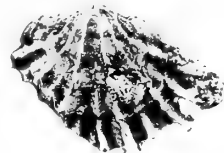
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PLATE 6

Schizophorella fallax (Salter) *silicis* subsp. nov.

FIG. 1. Interior of dorsal valve. BB.30225. $\times 1.6$.

Plectorthis ? *perditosulcata* sp. nov.

FIG. 2. Interior of incomplete dorsal valve. BB.30217. $\times 1.7$.

FIGS. 3, 4. Lateral and ventral views of ventral valve. Holotype, BB.30215. $\times 1.6$.

FIGS. 5, 8. Ventral fragment and damaged ventral valve, each showing small convex plate at apex of delthyrium. BB.30218 and BB.30220, $\times 3.6$ and $\times 2.2$, respectively.

FIG. 6. Exterior of dorsal valve. BB.30216. $\times 1.6$.

FIG. 9. Ventral fragment showing typical ornamentation. BB.30219. $\times 1.6$.

Platystrophia lutkevichi Alichova *contemplata* subsp. nov.

FIG. 7. Fragment of large ventral valve, showing ribbing pattern in sulcus. BB.30236. $\times 1.6$.

FIG. 10. Exterior of large dorsal valve. BB.30233. $\times 1.6$.

FIG. 11. Exterior of ventral valve. BB.30232. $\times 1.4$.

FIG. 12. Dorsal fragment, showing cardinalia and posterior adductor scars. BB.30237. $\times 1.8$.

FIGS. 13, 14, 18. Exterior, lateral and interior views of ventral valve. Holotype, BB.30231. $\times 1.5$.

FIGS. 15, 16. Dorsal fragment and broken dorsal valve showing ribbing pattern on fold. BB.30235 and BB.30234 respectively. $\times 1.5$.

Mcewanella dorsisulcata sp. nov.

FIG. 17. Ventral fragment showing features of interior. BB.30242. $\times 1.5$.

FIG. 19. Interior of dorsal valve. BB.30241. $\times 1.6$.

FIGS. 20, 21. Interior and exterior of dorsal valve. BB.30240. $\times 1.6$.



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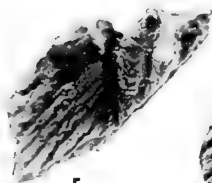
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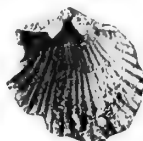
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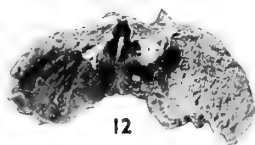
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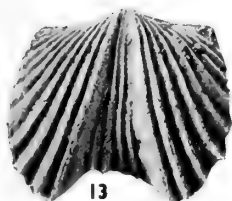
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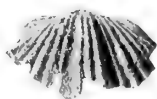
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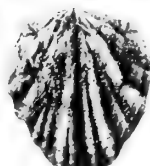
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PLATE 7

Mcewanella dorsisulcata sp. nov.

- FIG. 1. Exterior of damaged ventral valve. BB.30244. $\times 1.6$.
FIG. 2. Ventral fragment showing ornamentation. BB.30243. $\times 2.2$.
FIG. 3. Exterior of ventral valve. Holotype, BB.30238. $\times 1.4$.
FIG. 4. Exterior of ventral valve. BB.30239. $\times 1.5$.

Skenidioides cf. *asteroidea* (Reed)

- FIGS. 5, 6. Exterior and interior of ventral valve. BB.30250. $\times 4.1$.
FIGS. 7, 8. Interior and exterior of dorsal valve. BB.30251. $\times 4.3$.
FIGS. 9, 10, 11. Lateral, exterior and interior views of ventral valve with incurved beak. BB.30254. $\times 5.4$.
FIG. 12. Exterior of small dorsal valve. BB.30252. $\times 5.2$.
FIG. 13. Exterior of large ventral valve. BB.30253. $\times 2.4$.

Skenidioides paucicostatus sp. nov.

- FIGS. 14, 27. Exterior and interior of dorsal valve. BB.30248. $\times 5.1$.
FIGS. 15, 20. Anterior and ventral views of ventral valve showing bifurcating median rib. BB.30246. $\times 5.5$.
FIGS. 16, 17. Exterior and interior of ventral valve. BB.30247. $\times 5.4$.
FIGS. 18, 25. Interior and exterior of ventral valve. Holotype, BB.30245. $\times 5.4$.
FIGS. 19, 22. Exterior and interior of dorsal valve. BB.30249. $\times 4.5$.

Saukrodictya hibernica gen. et sp. nov.

- FIGS. 21, 23. Exterior and interior of damaged dorsal valve. Holotype, BB.30255. $\times 5.0$.
FIGS. 24, 26. Interior and exterior of broken ventral valve. BB.30257. $\times 5.2$.
FIGS. 28, 30. Interior and exterior of broken ventral valve. BB.30256. $\times 5.0$.
FIG. 29. Enlargement of Fig. 21, to show details of ornamentation. Holotype, BB.30255. $\times 9.0$.



PLATE 8

Rhactorthis sp.

- FIGS. 1, 2, 6. Exterior and two views of interior of dorsal valve. BB.30264. $\times 3.5$.
FIG. 5. Exterior of ventral valve, damaged marginally. BB.30266. $\times 3.8$.
FIG. 7. Interior of dorsal fragment, showing part of cardinalia, muscle field and digitate pallial sinus pattern. BB.30265. $\times 3.8$.

Scaphorthis sulcata sp. nov.

- FIG. 3. Exterior of dorsal valve. BB.30260. $\times 3.8$.
FIG. 4. Exterior of ventral valve. Holotype, BB. 30258. $\times 3.6$.
FIG. 8. Interior of ventral valve. BB.30259. $\times 2.7$.
FIGS. 9, 13. Two views of dorsal interior to show nature of cardinalia. BB.30262. $\times 2.8$.
FIG. 10. Exterior of broken dorsal valve. BB.30261. $\times 4$.

Dalmanella portranensis sp. nov.

- FIGS. 11, 12. Interior and exterior of dorsal valve. Holotype, BB.30267. $\times 2$.
FIGS. 14, 18, 19. Dorsal interior, exterior and oblique interior views of ventral valve. BB.30269. $\times 2$.
FIGS. 15, 16. Interior and exterior of dorsal valve. BB.30268. $\times 2$.
FIG. 17. Interior of ventral valve. BB.30270. $\times 2$.
FIGS. 21, 26. Exterior and interior of small dorsal valve. BB.30271. $\times 2.6$.

Isorthis ? *baillyi* sp. nov.

- FIGS. 20, 24, 29, 30. Anterior, dorsal, lateral and ventral views of complete shell. Holotype, BB.30273. $\times 2.5$.
FIGS. 22, 23, 27, 28. Dorsal, lateral, ventral and anterior views of complete shell. BB.30274. $\times 2.9$.
FIGS. 25, 31. Exterior and interior of dorsal valve. BB.30275. $\times 2.8$.

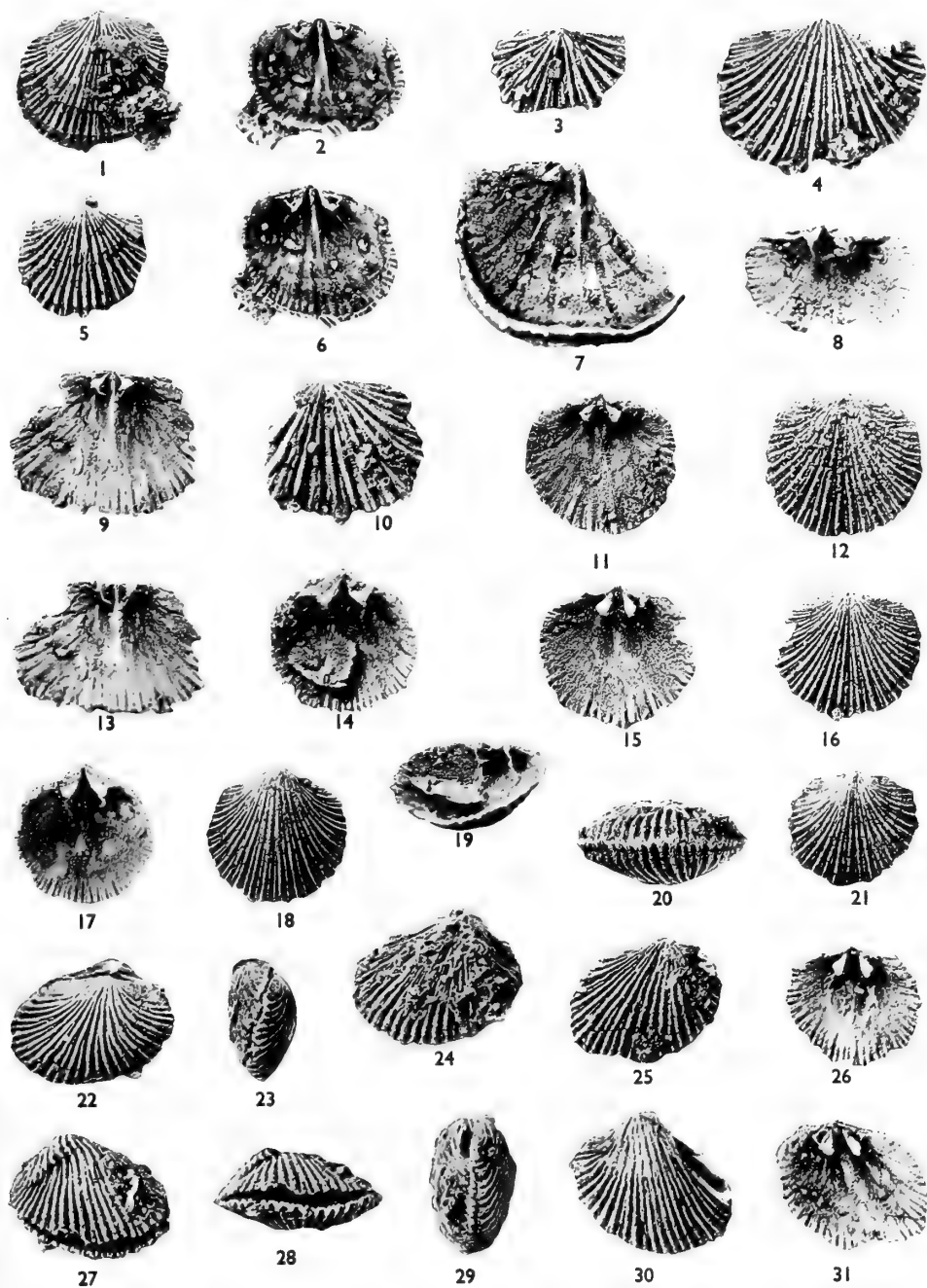


PLATE 9

Bancroftina sp.

FIG. 1. Exterior of dorsal valve. BB.30272. $\times 2.4$.

FIGS. 2, 4, 5. Ventral, postero-ventral and antero-ventral views of interior of same valve, to show muscle field and cardinalia. BB. 30272. $\times 2.4$.

Dicoelosia lata sp. nov.

FIG. 3. Exterior of ventral valve. BB. 30277. $\times 4.5$.

FIGS. 6, 9. Exterior and interior of dorsal valve. BB.30281. $\times 4.9$.

FIGS. 12, 15. Interiors of two ventral valves to show nature of muscle field. BB.30279 $\times 4.9$ and BB.30280 $\times 5.5$, respectively.

FIG. 14. Exterior of ventral valve. BB.30278. $\times 5.5$.

FIGS. 16, 17. Exterior and interior of dorsal valve. BB.30282. $\times 4.9$.

FIGS. 18, 19. Dorsal and ventral views of complete shell. Holotype, BB.30276. $\times 4.5$.

Reuschella sp.

FIG. 7. Ventral fragment, showing ornamentation. BB.30287. $\times 1.6$.

FIG. 8. Interior of broken ventral valve. BB.30286. $\times 1.5$.

FIG. 10. Interior of dorsal fragment. BB.30285. $\times 1.5$.

FIG. 11. Interior of broken dorsal valve. BB.30283. $\times 1.5$.

FIG. 13. Exterior of an asymmetrical dorsal valve. BB.30284. $\times 1.6$.

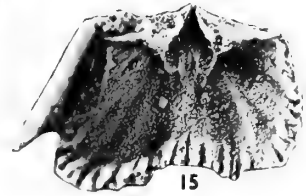
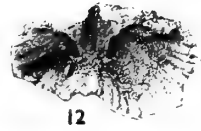
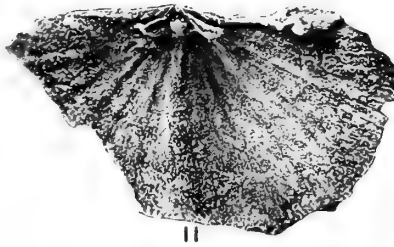
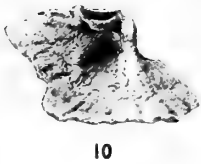
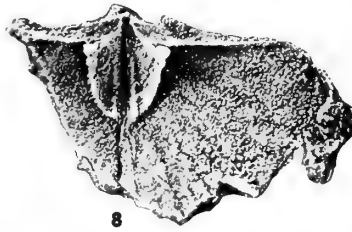
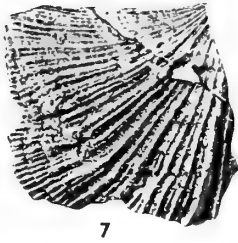
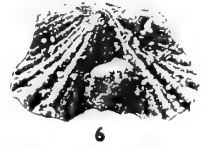
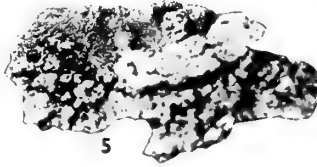
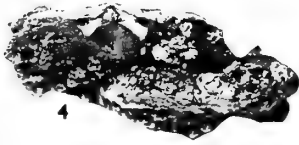
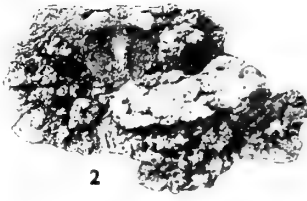


PLATE 10

Vellamo sulculata sp. nov.

- FIG. 1. Exterior of dorsal valve. BB.30296. $\times 2$.
FIG. 2. Interior of dorsal fragment, showing features of cardinalia. BB.30298. $\times 2$.
FIGS. 4, 8. Interarea and interior respectively of ventral valve. Holotype, BB.30292. $\times 2$.
FIG. 5. Interior of broken dorsal valve. BB.30295. $\times 2$.
FIG. 9. Interior of damaged dorsal valve. BB.30297. $\times 2.3$.
FIGS. 11, 12. Interior and exterior of ventral valve with broken deltidium. BB.30294. $\times 2.3$.
FIG. 14. Exterior of damaged ventral valve. BB.30293. $\times 2.3$.

Kullervo complectens (Wiman) *albida* (Reed)

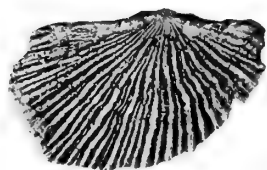
- FIGS. 3, 15, 16, 19. Ventral valve showing spondylium with subspondylial septa, and exterior from postero-ventral, posterior and oblique lateral views, respectively. BB.30330. $\times 2.8$, 2.6 , 2.4 , 2.6 respectively.
FIGS. 10, 13. Interior and exterior of dorsal valve. BB.30332. $\times 5$.
FIG. 20. Exterior of ventral valve, showing well-developed calcareous lip to foramen. BB.30331. $\times 4.1$.

Vellamo sp.

- FIGS. 6, 7. Interior and exterior of dorsal valve. BB.30299. $\times 4.7$.

Laticrura erecta sp. nov.

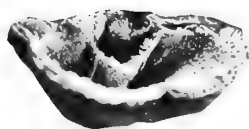
- FIG. 17. Interior of ventral fragment, showing apical plate and dental lamellae. BB.30291. $\times 2.9$.
FIG. 18. Antero-ventral view of dorsal interior, showing profile of brachiophore. Holotype, BB.30288. $\times 2.1$.



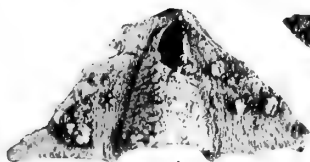
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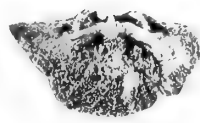
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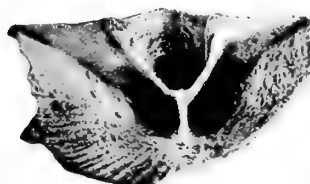
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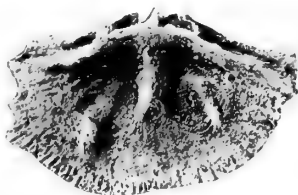
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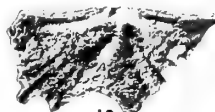
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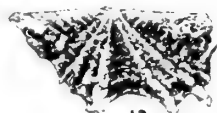
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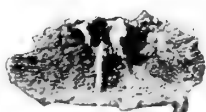
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PLATE 11

Triplesia cf. insularis (Eichwald)

FIGS. 1, 6, 7. Anteroventral and ventral views of exterior, and interior of ventral valve. BB.30333. $\times 1.4$.

FIG. 2. Exterior of damaged dorsal valve. BB.30334. $\times 1.4$.

FIGS. 9, 10. Interior and exterior views of dorsal hinge region to show features of cardinalia. BB.30335. $\times 4.7$.

FIG. 15. Fragment of dorsal valve, partly exfoliated to show internal features of fold. BB.30336. $\times 2$.

Streptis monilifera (M'Coy)

FIG. 3. Damaged dorsal valve, viewed posterodorsally. BB.30344. $\times 3.2$.

FIG. 4. Exterior of ventral valve. BB.30343. $\times 2.9$.

Oxoplecia cf. plicata (Wiman)

FIG. 5. Lateral view of broken dorsal valve showing thick nature of shell, particularly in posterior region. Only the inner and outer surfaces were altered during silicification, so that the original secondary shell substance between was dissolved by acid during etching, leaving a space as now seen in the specimen. BB.30339. $\times 1.4$.

FIG. 8. Exterior of ventral valve. BB.30337. $\times 2.1$.

FIGS. 11, 12. Exterior and interior of dorsal umbonal fragment to show cardinalia. BB.30340. $\times 1.9$.

FIG. 13. Exterior of broken dorsal valve. BB.30338. $\times 1.4$.

FIG. 14. Interior of broken dorsal valve, showing muscle and pallial markings. BB.30341. $\times 1.4$.

FIG. 17. Posterior view of ventral fragment showing interarea, teeth and pedicle foramen. BB.30242. $\times 2.1$.

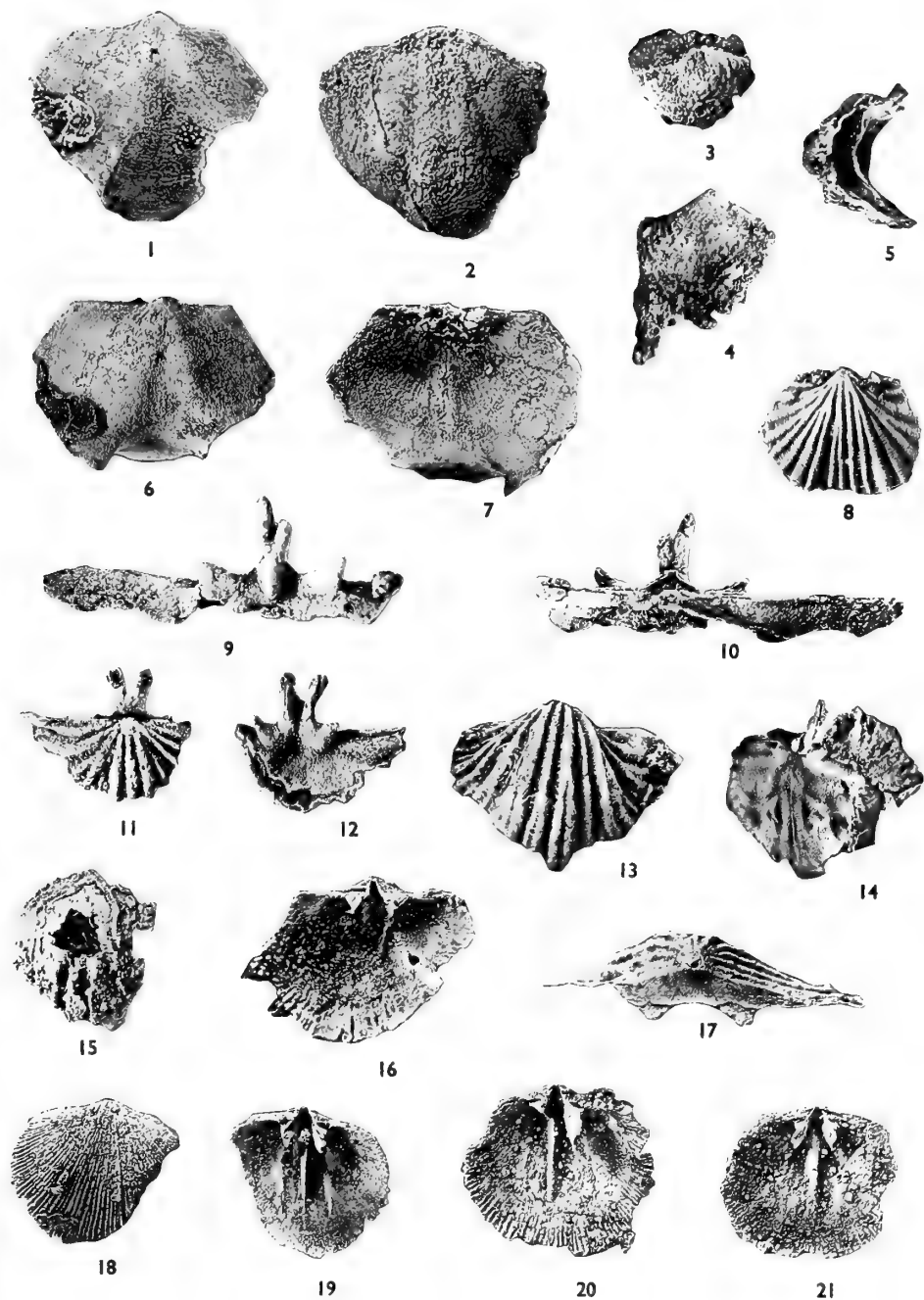
Laticrura erecta sp. nov.

FIG. 16. Interior of damaged ventral valve. BB.30292. $\times 2.8$.

FIGS. 18, 19. Exterior and interior of broken dorsal valve. BB.30289. $\times 2.1$.

FIG. 20. Interior of dorsal valve. Holotype, BB.30288. $\times 2.1$.

FIG. 21. Interior of dorsal valve. BB.30290. $\times 2.0$.





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THE GEOLOGY OF THE
ORDOVICIAN AND ADJACENT
STRATA IN THE SOUTHERN
CARADOC DISTRICT OF SHROPSHIRE

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 9 No. 7

LONDON : 1964

THE GEOLOGY OF THE ORDOVICIAN AND
ADJACENT STRATA IN THE SOUTHERN
CARADOC DISTRICT OF SHROPSHIRE



BY
WILLIAM THORNTON DEAN, Ph.D.

Pp. 257-296 ; 2 Plates ; 3 Text-figures

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THE GEOLOGY OF THE ORDOVICIAN AND ADJACENT STRATA IN THE SOUTHERN CARADOC DISTRICT OF SHROPSHIRE

By W. T. DEAN

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SYNOPSIS

The lithological and corresponding faunal subdivisions of the Ordovician rocks belonging to the Caradoc Series in south Shropshire are discussed and their outcrops in the district between Coston and Marshbrook shown on the accompanying maps. The Ordovician strata are involved in the major faulting of the Church Stretton Fault System, the main structural elements of which, established by Cobbold in the Comley area farther north, can now be traced both north and south of the Onny Valley. The Lawley Fault F₂, a low-angle reversed fault, is now believed to be the principal, and probably the earliest, structural line within the fault-system. Associated with it is The Cwms Fault F₃, essentially a tear-fault with sinistral displacement, involving little vertical movement. Although both F₂ and F₃ are mainly Taconian (late Ordovician to early Silurian) structures, they probably coincide with much earlier established lines of weakness dating from the Pre-Cambrian, and there was also recurrent movement along F₂ at least as late as the Lower Ludlow. The Church Stretton Fault F₁ is the latest of the major structures, at least post-Silurian in age although, from evidence elsewhere in Shropshire, involving intermittent rejuvenation as late as Triassic times. The effect of the Church Stretton Fault on Ordovician and Silurian sedimentation is believed to have been exaggerated, and it is

suggested that the Linley-Pontesford Fault System farther west was probably of more importance in this connexion. The relationship of the Ordovician to the Pre-Cambrian and Silurian rocks is described. As the result of excavations and field-mapping, particularly north of Horderley, the Western Longmyndian is held to be probably unconformable to the Eastern Longmyndian, thus confirming some of James's recent conclusions regarding The Longmynd itself.

I INTRODUCTION

SINCE the emergence of geology as a science, the portion of south Shropshire known as the Caradoc district, after the hill of the same name, has attracted the attention of numerous geologists and palaeontologists by reason of the wide diversity of rock-types, fossils and stratigraphical divisions found there. In particular, the publication of Murchison's "*Silurian System*" in 1839 gave a great impetus to research during the last century, and laid the foundations of later progress. Of Murchison's subdivisions of the Lower Palaeozoic strata the most important in the district is his "Caradoc Sandstone", a term originally embracing many of the rocks now included in the Caradoc Series of the Ordovician, together with others known now to be Pre-Cambrian and Lower Silurian in age (see Section VI).

In 1848 Ramsay & Aveline (p. 296) claimed that the, presumably, *Pentamerus* Limestone of the Llandovery Series was Caradoc in age; they were followed by Forbes (1848 : 299) who concluded that the marginal deposits of The Longmynd, now assigned to the Upper Llandovery Series, were of upper Caradoc age. Sedgwick (1852 : 142) noted the occurrence of *Ampyx* and *Trinucleus*, typical Ordovician trilobites, near Cheney Longville at a point where the Geological Survey had mapped Wenlock Shales, and in the same paper he separated the faunas of the "Caradoc Sandstone" at Horderley and May Hill, suggesting that the latter was the younger.

In a brief account of the Longmynd district Ramsay (1853 : 173) described what he called the Church Stretton Fault, extending for a distance of 45 miles and having a throw of 2,000 feet, south of Church Stretton. He believed the igneous masses of Caer Caradoc and The Lawley to be post-Silurian in age, and of the same period as the Church Stretton Fault; in addition he revised his previous (1848) interpretation of the "Caradoc Sandstones" bordering The Longmynd, and connected the beds with the Wenlock Shales.

The following year saw the first of several editions of Murchison's "*Siluria*", in which the author re-stated most of his beliefs as expressed in 1839. One of the most important works on the stratigraphy of south Shropshire appeared also in the same year when Salter & Aveline (1854) published the results of their investigations into the position of the "Caradoc Sandstone". Their still useful account demonstrated the unconformity at the base of the *Pentamerus* Beds, and divided the underlying rocks into five groups, of which two, the Hoar Edge Grits and *Trinucleus* Shales, received names. Unfortunately they failed to differentiate between the Harnage Shales and the Shineton Shales, with the result that their succession of the Caradoc Series put the Hoar Edge Grits above the Harnage Shales, a mistake which was perpetuated as recently as 1911 (Wade, table facing p. 446), even though Callaway had separated

the two groups of shales in 1877. The rest of Salter & Aveline's subdivisions were clearly described and localized, and there is little difficulty in following their account.

The One-Inch geological map published by the Geological Survey in 1855 indicated the line of the basal Silurian strata, and also the general course of the Church Stretton Fault, but no attempt was made to map the subdivisions of the Ordovician rocks. An additional dotted line marked the top of Murchison's original Caradoc Sandstone, and is discussed elsewhere in this paper (Section VI). The Pre-Cambrian rocks were shown as undivided "Cambrian", but the Silurian rocks of the Cwm Head district were recognized and their outcrop shown to be bounded by faults.

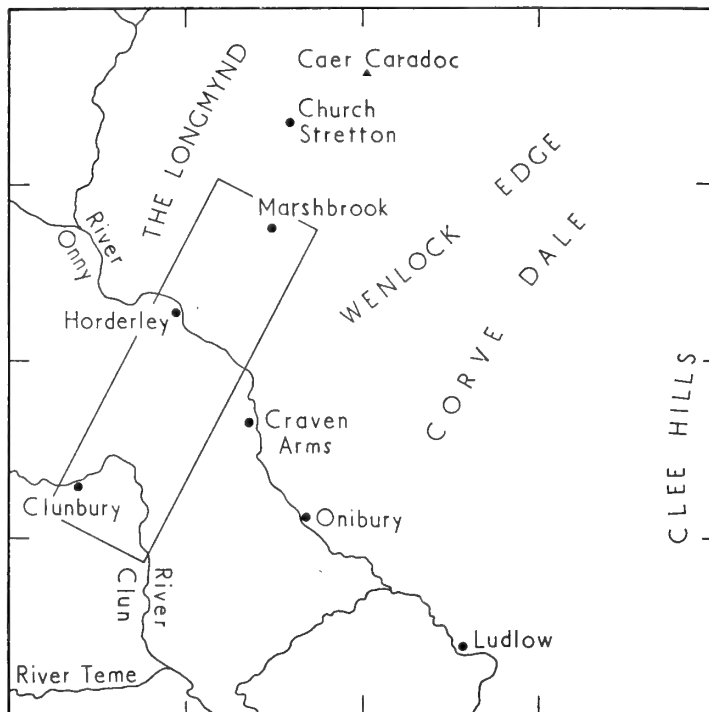


FIG. 1

A useful, though generalized, description of the area is contained in La Touche's (1884) "*Handbook of the geology of Shropshire*". Following Callaway (1877) the Hoar Edge Grits were placed in their true relative position, and La Touche (p. 23) also noted the differences of dip now known to occur on either side of The Cwms Fault F3, claiming that they were due to the "vast disturbance of the strata . . . a continuation of that . . . observed at Brokenstones". He also noted a quarry in a thick limestone of "Corston Grit-Bed" occurring in the River Onny valley and, farther upstream, a so-called Cambrian sandstone resting on "the last named". At this point his account became confused, and there appeared to be no proper appreciation of the unconformity between the Pre-Cambrian and Ordovician rocks.

In a short paper, the contents of which had been read to the British Association in the preceding year, Lapworth (1887 : 79) listed the Caradoc succession east of The Longmynd using the same stratal terms as La Touche, and in 1894 Lapworth & Watts (p. 316) repeated this succession with the addition of the subdivision "Acton Scott Beds" between the Longville (more correctly Cheney Longville) Flags and the *Trinucleus* Shales. The unconformity below the "Hoar Edge Grits" (strata now known to be at least partly equivalent to the Harnage Shales elsewhere) at Hope Bowdler was noted, and fossil lists for many of the Caradoc strata were given. Referring to the Hoar Edge Grits, the statement was made that "many of the same fossils (according to Lapworth) can be collected from calcareous bands in some of the volcanic rocks themselves"; the exact meaning of this was not made clear, but may have referred to the Neptunian dykes of the Hazler district near Hope Bowdler. The Acton Scott Beds were said to be especially important at Acton Scott "where they are associated with a peculiar igneous rock".

An extremely useful account of south Shropshire geology is that of Cobbold (1900). Unfortunately he did not include a geological map, but gave horizontal sections, together with the first, though brief, description of the main lines of structure which were to be further elucidated in his classic paper on the Comley district (Cobbold 1927). The faults F1 to F3 of the Church Stretton Fault System were noted, the last being described as the dividing line between regions of high and low dip.

In a series of papers between 1929 and 1949 Bancroft described numerous new species of brachiopods and trilobites from the type Caradoc Series, and attempted to subdivide the succession on the basis of the shelly faunas. More recently the Stages and Zones erected by him, and their correlation with the graptolite zones, have been reviewed and revised by the present author (Dean 1958) who has also given detailed faunal lists and descriptions of the trilobites (Dean 1960-63). Between 1925 and 1938 Whittard described the Llandovery and Wenlock rocks of the area in detail, together with their faunas; his papers included remarks on the general structure, though his published maps were confined to the Silurian outcrops. Since then, the same author has summarized the latest information available, including notes on structure and correlation (Whittard 1952; 1953). The most recent paper dealing with the structural geology of this part of south Shropshire is that of James (1956) who has mapped the Pre-Cambrian rocks of The Longmynd and given a new interpretation of their relationships. Confirmation of some of his views is proposed in the present paper.

The part of south Shropshire covered by the accompanying map (Text-fig. 1, Pls. 1, 2) follows the line of the Church Stretton Fault System from near Coston Farm, one mile east-south-east of Clunbury, the southernmost tip of the Ordovician outcrop, and extends in a strip about two miles wide to Marshbrook, by way of the Onny Valley between Horderley and Wistanstow. Mapping has been carried out on the six-inch scale, the relevant Quarter-Sheets of the Ordnance Survey map being Shropshire 55 SE, 63 NE & SE, 64 NW, 70 NW, NE, SW & SE. In addition, the areas around Wart Hill (known at one time as Wartle Knoll) and Brokenstones have been mapped on the scale of twenty-five inches to a mile. Frequent allusion is made

to the Caradoc district north-east of Marshbrook, and the area around Chatwall Hall, four and a half miles north-east of Church Stretton, has been mapped and described (Dean 1960a). Most of the field-work was carried out from the University of Bristol during the tenure of a Post-Graduate Research Scholarship awarded by the Shell Petroleum Company Ltd., to whom I tender my thanks, and some of the excavations in the Pre-Cambrian rocks were made with the help of a grant from the J. W. Young Fund of the Geologists' Association. Professor W. F. Whittard not only supervised the initial research, but has subsequently made many suggestions for the improvement of this manuscript and given me the benefit of his unique experience of Shropshire geology. Dr. Isles Strachan has kindly identified all the graptolites collected.

II STRATIGRAPHICAL SUCCESSION

Silurian System

LUDLOW SERIES

Upper Ludlow Shales	Dark grey-green shales and mudstones. Total thickness not seen.
"Aymestry Limestone"	Flaggy limestone bands and shales. Total thickness not seen.
Lower Ludlow Shales	Dark grey shales. Total thickness not seen.

WENLOCK SERIES

Cwm Head Limestone	Impure limestone and shales. 75 feet (estimated).
Wenlock Shales	Light grey shales and mudstones. <i>c.</i> 300 feet. <i>Major Disconformity</i>

LLANDOVERY SERIES

Purple Shales	Grey and purple shales and mudstones. 210 feet+.
<i>Pentamerus</i> Beds	Impure limestones with <i>Pentamerus oblongus</i> , and conglomerates at New House. <i>c.</i> 200 feet.
Arenaceous Beds	Conglomerates and grits. Total thickness not seen. <i>Unconformity</i>

Ordovician System

CARADOC SERIES

<i>Onnia</i> Beds	Grey and orange-weathering mudstones. 175 feet.
Acton Scott Beds (s.l.)	Grey mudstones and limestones, yellow-weathering calcareous sandstones. 200 feet.

Cheney Longville Flags	Green-brown, flaggy siltstones with limestone bands. Some yellow-grey mudstones in upper parts. Approx. 600 feet.
Alternata Limestone	Green-brown, siltstones, yellow sandstones, conglomerates and lenticular limestones with <i>Heterorthis alternata</i> . Up to 75 feet. <i>Local Unconformity</i>
Horderley Sandstone	Green and purple, massive and flaggy sandstones. North of the present map the lowest portion is represented by the Soudley Sandstone, and the middle portion by the Chatwell Sandstone (s.s.). c. 550 feet.
Glenburrell Beds	Dark, brown-green mudstones with occasional impure limestone bands. c. 200 feet.
Smeathen Wood Beds	Yellow-weathering, sandy, calcareous mudstones. 130 feet.
Coston Beds	Sandstones and conglomerates with occasional shell-banks. Up to 110 feet. <i>Unconformity</i>

Pre-Cambrian rocks

	WESTERN LONGMYNDIAN or WENTNOR "SERIES" <i>pars</i>
? Bayston-Oakwood Group	Maroon sandstones and conglomerates. Thickness unknown. <i>Unconformity</i>
	EASTERN LONGMYNDIAN or STRETTON "SERIES" <i>pars</i>
Stretton Shales and, probably, Buckstone Rock	Green-grey, slickensided shales. Thickness unknown.
	URICONIAN
Eastern Uriconian	Undifferentiated group of tuffs, agglomerates, felsites and rhyolites. Thickness unknown.

III PRE-CAMBRIAN ROCKS

In south Shropshire, Pre-Cambrian rocks form an elongated inlier about five miles long extending north-eastwards from Aston-on-Clun, $2\frac{1}{2}$ miles west-south-west of Craven Arms, by way of the River Onny valley near Horderley, as far as Cwm Head, near Marshbrook. Generally speaking, the rocks are bounded to the west by the Church Stretton Fault, known also as F1 using the terminology established by Cobbold (1927), and to the east by the unconformable base of the Ordovician strata, but as they have been affected by the whole of the Church Stretton Fault System they may also be found abutting against Silurian strata.

The subdivisions of the Pre-Cambrian present in south Shropshire, after Whittard (1952 : 145), are as follows :

{	Wentnor " Series "	{	Bridges Group
	(= Western Longmyndian)		Bayston-Oakswood Group
{	Stretton " Series "	{	Portway Group
			Lightspout Group
			Synalds Group
			Burway Group (with Buckstone Rock)
			Stretton Shales
{	Eastern and Western Uriconian	{	Helmeth Grits

More recently James (1956) termed these " Series " the Strettonian and Wentnorian respectively, and separated the Portway Group under the name Mintonian, though Greig & Wright (1959 : 30) have shown the latter term to be no longer usable.

(i) URICONIAN

The oldest of the Shropshire Pre-Cambrian rocks are so named after the Roman settlement of Uriconium, 5 miles east of Shrewsbury. They crop out along either side of The Longmynd where they are known respectively as Eastern and Western Uriconian, the two groups being thought to be of similar age (James 1956 : 316). The Eastern Uriconian rocks form the Church Stretton Hills, a line of prominences running roughly south-west and extending from Lilleshall Hill and The Wrekin in the north, to Wart Hill in the south. The only Uriconian outcrops concerned in the present map occur to the north of Hopesay and are three in number. The rock types include tuffs, felsites and agglomerates, but they are mapped here as undifferentiated Uriconian.

The southernmost outcrop occurs in the stream about 400 yards south of the hamlet of Round Oak ; it is apparently small and structural relationships are not clear. The rocks, mainly tuffs, appear to form a small, discontinuous ridge in the bank to the east of the stream and are interpreted as having been brought into juxtaposition with the Western Longmyndian of Hopesay Hill by the southernmost extension of The Lawley Fault F2.

The conical promontory of Wart Hill itself is composed entirely of Uriconian rocks which stand out sharply from the adjacent, more easily eroded Western Longmyndian arkoses and sandstones. The north-western and south-eastern boundaries of the hill follow relatively straight lines which have been mapped as part of the structural line of F2 by analogy with the area immediately to the north. The hill is surrounded on all sides by scree which mask the junctions and relationships of the rocks, and it is possible that the Western Longmyndian/Uriconian junction on the north-eastern and south-western flanks of Wart Hill may be unconformable.

To the north-east of Wart Hill the Uriconian rocks of Palace Coppice form a pronounced ridge running north-eastwards. Exposures are few and the structural relationships are once again obscure, but the outcrops appear to be bounded by faults forming part of the line of F2.

(ii) STRETTON "SERIES" or EASTERN LONGMYNDIAN

The only part of the Eastern Longmyndian or Strettonian succession known to be involved within the bounds of the map is that of the Stretton Shales, though the succeeding Buckstone Rock, at the base of the Burway Group, may be present. Near Church Stretton the Stretton Shales have been divided into two groups, a lower, the Watling Shales, and an upper, the Brockhurst Shales. These names refer to the outcrops of Stretton Shales situated respectively on the western and eastern sides of the Church Stretton Fault Fr, but Cobbold & Whittard (1935 : 355) have emphasized that it is almost impossible to differentiate between the two, which probably constitute one, almost homogeneous, series. James (1956 : 317) has, however, retained the twofold subdivision and pointed out that the Watling Shales are generally purple and green whilst the Brockhurst Shales are grey and green.

In and near the Onny Valley the Strettonian rocks comprise hard, compact, grey-green mudstones and shales, sometimes with calcareous concretions exhibiting cone-in-cone structure ; their lithology and colour agree best with those of the Brockhurst Shales. The beds are almost invariably contorted, shattered and jointed, often with numerous quartz veins, particularly near Horderley where the outcrops are in close proximity to the Church Stretton Fault.

In the southern part of the map the Stretton Shales are first seen at the south end of Dunslow Hollow, north-north-west of Wart Hill. There they abut against Western Longmyndian arkoses but owing to the deep weathering of the junction, excavations to determine whether a fault or an unconformity is present have proved inconclusive. Grey, siliceous, jointed shales are exposed at several points in Dunslow Hollow and in the north-western part of neighbouring Harps Dingle, whilst at Heath Wood they are overlain unconformably by a capping of Coston Beds (basal Caradoc Series). The Stretton Shales, being relatively easily eroded, form a tract of low-lying, often marshy ground extending north-north-east from Lower Carwood to Horderley, parallel to the ridge of Western Longmyndian sandstones immediately to the south-east, against which they are faulted. The beds are well

exposed near Horderley, especially in the eastern side of the road to Marshbrook, where they are much disturbed and slickensided, with variable dips. They form the greater part of the valley between Horderley and Brokenstones, which is excavated through the overlying Western Longmyndian sandstones, and their outcrop extends as far north as near Pillocksgreen.

(iii) WENTNOR "SERIES" or WESTERN LONGMYNDIAN

The rock-types included in the Western Longmyndian of the present map consist almost entirely of maroon or purple sandstones and arkoses, and may be equated tentatively with part of the Bayston Group or Bayston-Oakwood Group, the lowest of the subdivisions of the Western Longmyndian recognized respectively by the Geological Survey (Pocock *et al.* 1938 : 47) and Whittard (1952 : 145).

The southernmost outcrops occur near, and north of, Aston-on-Clun where Western Longmyndian sandstones form the "hog's back" of Hopesay Hill. Although sandstone débris is everywhere abundant, solid exposures are, unfortunately, rare and in the absence of marker horizons it has not proved possible to elucidate the structural features which undoubtedly exist within the bounds of the hill. Small-scale working of some of the sandstones has been carried on in the past but all the old diggings are now overgrown. Exposures of arkose can be seen in the west side of the cart-track 1,000 feet north-north-east of the road-junction at Hopesay village, and in the west side of the road to Round Oak 1,000 feet north-east of the same road-junction, but dip readings there have not proved reliable.

Along the north-eastern side of Hopesay Hill the outcrop of the Western Longmyndian is bordered to the east by a fault which, at Sibdon Cottage and Hammondsgreen, brings it into contact with Ordovician strata, probably part of the Smeathen Wood Beds. East of Wart Hill, at Urwicks Wood and northwards to Palace Coppice, Western Longmyndian sandstones are affected by the line of The Lawley Fault F2. Exposures are generally poor but vertical beds are visible in the stream bed 400 feet south-south-east of Palace. In the strip of ground centred on Wart Hill, extending north-eastwards and bounded by part of the line of F2, sandstones and arkoses are abundant but in no instance has the contact with the Uriconian been seen. As stated earlier, the Western Longmyndian on the north-eastern and south-western flanks of Wart Hill may be unconformable to the Uriconian, and lower, arkosic beds may possibly be present.

The ground from Round Oak to Upper Carwood is occupied by sandstones, the outcrop of which then extends northwards into Dunslow Hollow in the form of a long "neck", marked in the field by a feature. The eastern boundary of this is almost certainly a fault, but the western limit may be in the form of an unconformable junction although, again, the actual contact is not seen.

North-north-eastwards from Heath Wood, sandstones of Western Longmyndian age form a prominent ridge, bounded on the west by the line of F2 and on the east by unconformable Coston Beds. At the sharp bend in the River Onny, 400 yards south-east of Horderley station, there are numerous exposures near the junction of the two Longmyndian groups. Grey shales are seen at the western, and dark-red

sandstones at the eastern end of the outcrop, and between the two are maroon shales. The mutual relationships of the rocks are not clear, and it is difficult to assess which of the Longmyndian groups should contain the maroon shales, but for the present they are referred to the Western Longmyndian. In the Longmynd area the Bayston Group is followed by purple shales and mudstones of the Bridges Group, and it is possible that part of the latter may be represented, whilst one of the excavations north of Horderley, described later (Excavation A) in this paper, contains maroon shales of probable Western Longmyndian age.

The ridge of Western Longmyndian rocks continues north-eastwards from the River Onny, and about 20 feet of strata are exposed in an old quarry 1,300 feet east-north-east of Horderley station; at this point the rocks are purple-grey, fine-grained sandstones, well jointed (100° – 280°) and dipping west at 55 degrees. About 2,000 feet north-east of the same quarry this outcrop of Western Longmyndian is terminated by an almost east-west fault, to the north of which is a small "block" of similar strata, bounded on its southern and north-eastern sides by faults but probably overlain unconformably by Coston Beds of the Caradoc Series on the north-western side. Western Longmyndian rocks are seen also in the floor of the Horderley-Marshbrook valley where four outcrops occur between Brokenstones and Pillocksgreen (see later).

(iv) THE RELATIONSHIP OF THE TWO LONGMYNDIAN "SERIES"

The area north-east of Horderley is interesting for the evidence it affords regarding the mutual relationship of the Eastern and Western Longmyndian rocks. This has been uncertain for many years, and owing to the almost invariably poorly exposed junction most conclusions have been founded solely on inference.

Late in the nineteenth century Blake (1890 : 388) claimed that the "basal Cambrian" (= Western Longmyndian) was unconformable to what he called the "Monian" (= Eastern Longmyndian). Cobbold (1900 : 114) agreed that such an unconformity existed, but accepted it only at the base of the Ratlinghope Conglomerate, disagreeing with Blake's contention that it occurred also at the base of the Huckster Conglomerate (the lowest horizon within the Portway Group). Cobbold & Whittard (1935 : 356) expressed the view that, on account of its wide geographic distribution and the fact that it alone is overlain by Cambrian rocks, the Western Longmyndian may be presumed to have acted as an unconformable mantle which covered the Eastern Longmyndian rocks during Cambrian and Ordovician times. Challinor's suggestion (1948 : 107) that exposures in the Longmyndian rocks of Haughmond Hill, 3 miles north-east of Shrewsbury, indicate that the Eastern Longmyndian there overlies the Western Longmyndian unconformably has been shown by Whitehead (1948 : 181) to be untenable. More recently part of The Longmynd itself has been mapped in detail by James (1956) who has postulated the presence there of two unconformities within the Longmyndian succession, *a.* at the base of the Portway Group, and *b.* at the base of the Bayston Group. The former, and less convincing, of these was put forward mainly to account for certain unusual features of the geology at Deadman's Batch, $2\frac{1}{2}$ miles

MAP OF THE BROKENSTONES- CWM HEAD DISTRICT

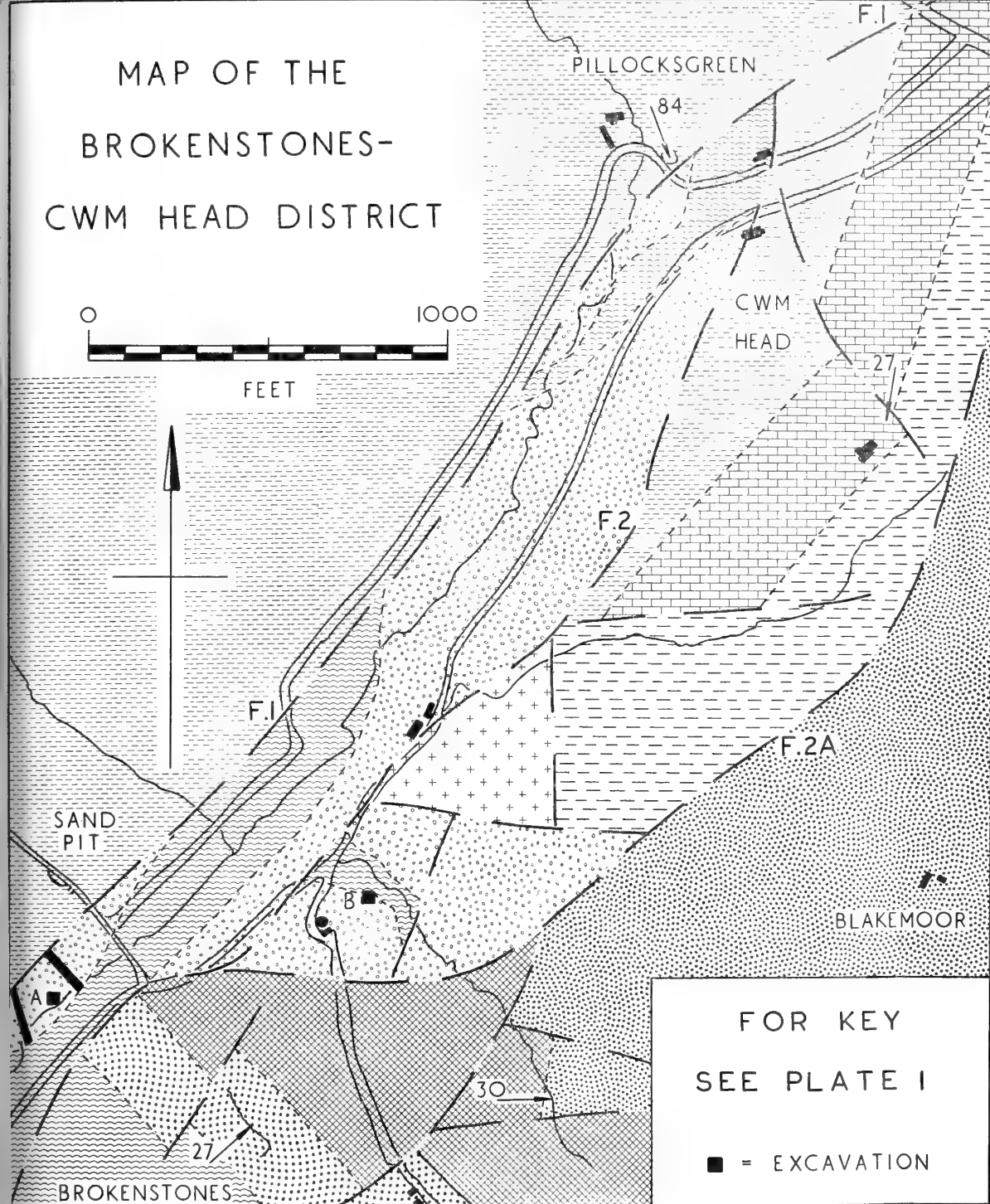


FIG. 2

north-north-east of Church Stretton, and its existence has not been accepted by Greig & Wright (1959 : 30). Unconformity *b.*, however, may be regarded as being important and of great magnitude.

In 1953 Professor Whittard (p. 247) referred to the possibility of demonstrating the existence of an unconformity at the base of the Western Longmyndian near Brokenstones, $\frac{1}{2}$ mile north-east of Horderley, and subsequent investigations were commenced under his supervision by a Field Mapping Class from the University of Bristol. Since then, both during and after the writer's mapping of the district on the six-inch and twenty-five-inch scales, the area has been further investigated, the preliminary excavations have been enlarged, and the results are given below. Although excavations have been started at several points in the district only two have yielded critical information ; they are designated A and B in the following account.

Excavation A.

This, the larger of the excavations, was made in the north-western bank of the stream 300 feet almost due south of the so-called "Sand Pit" (actually a small quarry in Wenlock Shales) to the north-west of Brokenstones (see Text-fig. 2). Almost at stream-level were found jointed, grey-green shales, of which only 1 to 2 feet were seen, exhibiting in parts a cherty appearance suggestive of the Buckstone Rock near Church Stretton, an horizon into which the Brockhurst Shales, the upper subdivision of the Stretton Shales, grade upwards. The shales are overlain by dark-red to maroon shales, 2 feet thick at this point but between 3 and 4 feet thick when seen farther upstream. The two groups of shales are separated by a small band of fault-gouge, calcite and breccia, at most only a few inches thick, and the latter is taken to represent a small fault-plane which, as far as can be ascertained, dips to the north-west at about 45 degrees. The maroon shales are followed, apparently conformably, by $4\frac{1}{2}$ feet of a conglomerate which contains pebbles, up to 4 or 5 cms. in diameter, of quartz, quartzite, Uriconian felsite and rhyolite. The topmost beds of the exposure, higher in the stream bank, have not been seen in their entirety, but they include more than 3 feet of coarse maroon sandstone. The section may be summarized as follows :

	Individual Thickness ft. ins.	Max. Total Thickness ft. ins.
Maroon sandstone	3 3	3 3
Maroon conglomerate	5 2	8 5
Red-maroon shales	2 4	11 2
	to 2 9	
Fault breccia, etc.	0	11 6
	to 4	
Grey-green shales	1 8	13 2

The grey-green shales are considered to belong to the Brockhurst Shales or Buckstone Rock. The conglomerate and overlying sandstones are typical, in both colour and abundance of contained Uriconian material, of the Bayston Group

(Wentnor "Series"), a subdivision which comprises purple grits and shales as well as three persistent conglomerate horizons (Pocock *et al.* 1938 : 47). The position of the maroon shales is more difficult to assess but the writer is unaware of any locality on The Longmynd where the Eastern Longmyndian rocks include similar green and red shales at corresponding levels. If the maroon shales were of Eastern Longmyndian age they would necessarily belong to a much higher horizon than the Buckstone Rock, and the fault which here separates the two lithologies would need to be a much larger structure than it appears to be in the field, with an extremely large throw. It is believed that the maroon shales, together with the overlying conglomerates and arenaceous beds, are Western Longmyndian in age and unconformable to the Eastern Longmyndian. Immediately to the north-east of the excavation, and farther to the south-west, the Western Longmyndian outcrop is cut by two dolerite dykes which run approximately north-west-south-east (see later).

Excavation B.

Additional evidence of the unconformity at the base of the Wentnor "Series" is adduced from an important exposure in the stream-section nearly 200 feet north-north-east of Round House, Brokenstones (see Text-fig. 2). At this point jointed, grey-green shales, believed to belong to the Brockhurst Shales, are seen in the south-western bank of the stream, dipping steeply in an approximately south-westerly direction. They are overlain unconformably by a well-developed conglomerate consisting of angular to sub-rounded fragments which are poorly sorted and include pebbles up to 2.6 cms. in diameter. The small amount of matrix present is purple in colour and most of the derived fragments appear to be of Uriconian material, including quartz, quartzite, rhyolite and felsite, though there are some of grey-green shales (? Stretton Shales) which have been heavily slickensided. The conglomerate is different in appearance from the basal Llandovery conglomerates which abound in the Caradoc District and on lithological grounds is assigned to the Western Longmyndian. The section in the stream-bank extends north-westwards downstream, and in this direction the conglomerate/shale junction first descends from the top of the bank to below the stream bed and then, about 20 feet downstream, reappears and ascends the bank. The general impression is of a "pocket" of conglomerate, at least 9 to 10 feet thick, filling a hollow eroded in the Stretton Shales. It is unlikely that the pocket-like cross-section is the result of folding because, at its south-eastern extremity, the conglomerate is followed, apparently conformably, by a well-cemented maroon sandstone, typically Western Longmyndian in character and 10 to 15 inches thick, which overlaps the conglomerate and comes to rest on the grey shales. The presence of the sandstone is believed to afford additional evidence for the Western Longmyndian age of the conglomerate, which is thought to be identical with others cropping out near Round House and forming part of an outcrop some 600 feet by 400 feet. The stream north-east of Round House has excavated what is virtually a small inlier of Eastern Longmyndian shales, but the outcrop is truncated on its eastern side by a small, north-north-easterly

fault which brings these strata into juxtaposition with maroon sandstones thought to be Western Longmyndian in age, probably from an horizon later than the conglomerate. The Wentnorian conglomerates of the Brokenstones district correspond broadly to the Haughmond Conglomerate at the base of the Bayston Group, though it would be unwise to attempt a direct correlation over a long distance using rocks of this type.

The remaining Western Longmyndian rocks of the Horderley-Marshbrook valley comprise a small outcrop near Pillocksgreen and another, larger outcrop extending from near Brokenstones as far as Cwm Head Church (see Text-fig. 2). In this neighbourhood the elongated outcrop of both Eastern and Western Longmyndian strata is bounded on the north-west by the Church Stretton Fault F₁, and on the south-east by the southern extension of The Lawley Fault F₂. The rocks are predominantly purple or dark-red, coarse-grained sandstones, but several patches of conglomerate occur and contain abundant Uriconian material, including pebbles up to 6.5 cms. in diameter. The two outcrops of Western Longmyndian are separated on the map by a narrow strip of Brockhurst Shales. This is interpreted as resulting from the excavation of the lower part of the valley through the unconformably overlying Western Longmyndian rocks. The junction of the two groups has not been seen here, though it is believed that the plane of the unconformity is variable but dips only gently westwards at this point. The alternative possibility of a faulted relationship between the Eastern and Western Longmyndian rocks would require the presence of two almost parallel faults of enormous throw in order to bring the appropriate horizons into juxtaposition, and this is considered unlikely in view of the uncrushed condition of the rocks.

The line of unconformity shown by James (1956 : 316) to exist at the base of the Bayston Group was said by him to be creeping eastwards at the expense of the Portway Group. The evidence of the Horderley-Marshbrook valley confirms the profound nature of the break and suggests that between The Portway, the ancient road running along the crest of The Longmynd, and Brokenstones, a distance of some 2½ miles, the base of the Wentnor "Series" has transgressed rocks of the Stretton "Series" whose combined thickness must be of the order of 10,000 feet.

IV. ORDOVICIAN ROCKS

In south Shropshire, Ordovician strata other than those belonging to the Caradoc Series are unknown, and the latter are separated by large stratigraphical breaks from both the underlying and overlying rocks. The succession of lithological subdivisions within Murchison's type section of the Caradoc Series in the Onny Valley south-east of Horderley, together with the corresponding faunal stages introduced by Bancroft and recently revised (Dean 1958), is shown below in simplified form.

(i) Coston Beds

In the vicinity of Coston Farm, from which they take their name, the Coston Beds may be divided into three parts. The lowest comprises well-developed basal

LITHOLOGICAL SUBDIVISION		STAGE	
Onnia Beds		Onnian	
Acton Scott Beds (<i>s.l.</i>)		Actonian	
Cheney Longville Flags	{ Upper	Marshbrookian	
	{ Lower	Upper	} Longvillian
Alternata Limestone			
Horderley Sandstone	{ Upper	Lower	
	{ Middle		
	{ Lower		
		Soudleyan	
Glenburrell Beds		Harnagian	
Smeathen Wood Beds			
Coston Beds		Costonian	

conglomerates, their thickness variable but up to 50 feet, in which fossils have not yet been found. They are seen in the quarry north-east of The Hollies ; in the series of disused quarries at and near Quarry House, north of Coston Hall ; and in the small quarry $\frac{1}{2}$ mile south-south-east of Coston Farm. Higher in the succession the conglomerates give way to sandstones, occasionally conglomeratic, containing lenticular shell-beds full of brachiopods, especially *Harknessella vespertilio* (J. de C. Sowerby), *H. jonesi* Bancroft, *Heterorthis patera* (Davidson) and *Dinorthis flabellulum* (J. de C. Sowerby). A notable feature is the large number of quartz-pebbles often occurring with the brachiopods. To these strata the name "*Harknessella* Beds" has been given, and they are particularly well exposed in the small quarry 40 yards east-south-east of The Hollies, as well as in and near the road-cutting 100 yards due east of Coston farmhouse, where they are extremely fossiliferous. Trilobites are rare in the *Harknessella* Beds and include only an occasional *Flexicalymene* sp. and asaphid.

The highest Coston Beds, the *Costonia ultima* Beds, may be examined at and near the disused quarry about 200 yards south of Coston Farm ; they comprise massive, calcareous sandstones, generally deeply weathered, throughout which fossils are evenly, and often abundantly, distributed. The maximum thickness is about 40 feet and the fauna includes the eponymous trilobite *Costonia ultima* (Bancroft) together with *Flexicalymene* cf. *acantha* Bancroft, the ostracod *Tallinnella scripta*

(Harper), and the brachiopods *Dinorthis robusta* Bancroft, *Orderleyella plicata* Bancroft and *Smeathenella strophomenoides* Bancroft. Generally the Coston Beds follow the regional south-easterly dip, but some north-westerly dips occur near the line of the Church Stretton Fault F1.

To the north of the Coston Inlier the Coston Beds emerge from beneath the Alluvium of the Clun Valley at Aston-on-Clun in an attenuated form. Their outcrop runs along the south-eastern slopes of Hopesay Hill where they rest unconformably on Western Longmyndian rocks, and the basal conglomerates may be seen, dipping south-east, at and near Oldfield farm where they were once extensively quarried. Farther north, near Sibdon Carwood, the outcrop narrows and is finally truncated by an almost north-south fault, the Sibdon Cottage Fault, which meets The Lawley Fault F2 a little way to the north. The beds are seen next about 700 yards north of Wart Hill where they form the promontory of Heath Wood and rest on Stretton Shales of the Eastern Longmyndian; disused small quarries are numerous there and the outcrop is involved in the faulting of the Wart Hill complex. The much-jointed basal conglomerates are seen in the track west of Wood House, and near the southern end of Smeathen Wood where they rest on Western Longmyndian beds. Conglomerates and sandstones also form a well-marked ridge north of Wood House, broken at intervals by small dip faults and running north-north-east along the strike towards the River Onny.

Near the south bank of the River Onny the large disused quarry 380 feet south-west of Round House exposes about 70 feet of massive, calcareous sandstones, the topmost beds containing occasional specimens of the brachiopod *Salopia salteri* (Davidson). The contact of the Western Longmyndian and the Caradoc Series may be seen there, and its nature has been discussed by Whittard (1953: 243) who claims that it is faulted. The writer agrees with this view, and mapping suggests that a small fault has cut out at least the basal conglomerates of the Coston Beds. North of the fault the outcrop is displaced to the north-east and the beds are exposed at Rock Cottage, just west of Glenburrell, where they dip steeply south-east. The rock is a calcareous sandstone with several conglomeratic bands, contains abundant shelly material including *Dinorthis flabellulum*, and may possibly be correlated with part of the Middle Coston Beds. The outcrop continues in a north-easterly direction until truncated by a roughly east-west fault which displaces the Coston Beds so that they form an outlier at and near Brokenstones Plantation. There the Upper Coston Beds contain the characteristic fossils, especially *C. ultima*, in fair abundance, together with occasional survivors, such as *Dinorthis flabellulum* and *Heterorthis patera*, from earlier horizons.

No other outcrops of Costonian age are known in the southern Caradoc district, but in the area north of the Cardington Hills the succession shows differences in both lithology and faunas. Flaggy, sandy limestones with *Harknessella* are well developed, though the species are different. At least one shale horizon has been found, with graptolites indicating the zone of *Nemagraptus gracilis*, and *Costonia ultima* is replaced by *C. elegans* Dean. The stratigraphy has previously been discussed in some detail (Dean 1958; 1960).

(ii) Smeathen Wood Beds

The Coston Beds of the southern Caradoc district are succeeded conformably by the Smeathen Wood Beds. The latter are so named after the type-locality south-east of Horderley, and in the past they and the succeeding Glenburrell Beds have generally been grouped together under the name "Harnage Shales". Lithologically the Smeathen Wood Beds comprise yellow-weathering calcareous mudstones with some grey-green shales, and are divisible into two successive trilobite zones of *Reuscholithus reuschi* and *Salterolithus caractaci*, subdivisions which together form the lower two-thirds of the Harnagian stage.

On the accompanying map the southernmost outcrops occur in the neighbourhood of Sibdon Carwood, where the beds are affected by faulting and are overstepped by the Wenlock Shales; exposures are poor as the outcrop is obscured by the glacial drift of the Craven Arms district. The horizon must, however, have extended farther south as is shown by the presence, in an old collection at the British Museum (Natural History), of two specimens of *Kloucekia harnagensis* (Bancroft) labelled "Coston". The matrix is that of the Smeathen Wood Beds but contains some sub-angular quartz pebbles. In an old quarry, marked as "Gravel Pit" on the six-inch O.S. map, one-third of a mile north-west of Castle Farm, Sibdon Carwood, strata low in the succession are seen. They consist of vertical grey shales striking north-south, associated with a lava flow of trachybasalt. The locality has been mentioned by Whittard (1952 : 162) who reported unidentifiable graptolites from the shales. The lava flow can be traced southwards to a point east of Oldfield Wood, where it has been quarried; immediately to the west is another, smaller quarry where a second older lava has been worked, but it has not proved possible to trace the latter for more than a few yards. Higher beds of mudstone, dipping east at 65 degrees, are exposed about 300 yards north-west of Castle Farm, opposite the reservoir, and similar beds occur in the wood south-east of Sibdon Cottage.

In the western slopes of the small valley immediately north of the cottage called Hammondsgreen, by Long Lane, grey-green shales are faulted against Western Longmyndian sandstones. Farther north the beds become involved in the faulting near Wart Hill which cuts out part of the Caradoc succession, and they are only poorly exposed until the southern end of Smeathen Wood is reached. The section in the old cartway in the plantation south-west of Wood House has yielded a good fauna of early Harnagian age, including *Reuscholithus reuschi* Bancroft, *Smeathenia smeathenensis* (Bancroft), *Kloucekia harnagensis* (Bancroft), *Flexicalymene acantha* Bancroft, *Primaspis harnagensis* (Bancroft), *Proetidella fearnsidesi* Bancroft, *Salopia salteri* (Davidson) and *Smeathenella harnagensis* Bancroft, with gastropods (*Cyrtolites*, *Phragmolites*), conulariids, ostracods (*Tallinnella scripta* Harper sp.) and machaeridia. The direction of the dip is about north-east but the amount is difficult to measure as the rocks are jointed and broken. Their outcrop is marked by a hollow extending towards the River Onny, parallel to the ridge of Coston Beds north of Wood House described earlier, and they have been seen, though poorly exposed, at and near the south-eastern end of the quarry by the south bank of the river, 380 yards south-west of Round House.

North of the River Onny, exposures of the Smeathen Wood Beds are uncommon but grey shales, dipping steeply eastwards, are visible about 300 yards north-north-east of Glenburrell Farm. In this neighbourhood Bancroft (1949 : 294) proved the presence of the *Salterolithus caractaci* Zone by means of excavations 700 feet north of Glenburrell Farm.

To the north-west of Woolston sandy mudstones have yielded trilobites of the basal Harnagian, especially *Smeathenia smeathenensis*, and suggest a slightly more arenaceous facies than at the southern end of Smeathen Wood. Nearby, close to the " Spring " on the six-inch O.S. map, 1,850 feet south-south-east of Round House, Brokenstones, flaggy sandstones have yielded *Kloucekia harnagensis*, *Smeathenella harnagensis* and *Tallinnella scripta*, and so represent the lowest Smeathen Wood Beds. At this point the outcrop is truncated by an easterly transverse fault and the strata abut against Western Longmyndian sandstones.

Shales of the Smeathen Wood Beds crop out in the dingle section north-east of Brokenstones (see Text-fig. 2) ; the exposures are partly overgrown but the beds are seen dipping steeply east, and are affected by faulting of the Brokenstones complex. Similar beds possibly occupy the low-lying ground beneath the scarp of Horderley Sandstone north-east of Brokenstones, but have not been seen. There is room for outcrops of Smeathen Wood Beds overlying the Coston Beds of Brokenstones itself, but they are not exposed and have been marked only tentatively on the map.

(iii) Glenburrell Beds

These strata, named after Glenburrell Farm, Horderley, comprise dark-green mudstones and shales with occasional impure limestone bands. They are equated with the topmost trilobite zone of the Harnagian, that of *Broeggerolithus* [*Ulricholithus*] *ulrichi* (Bancroft), together with the zone of *Broeggerolithus broeggeri* (Bancroft) of the Lower Soudleyan. They form, in effect, a continuation of the phase of mudstone sedimentation which commenced with the lowest Smeathen Wood Beds and ended immediately below the lowest Horderley Sandstone. The rocks weather easily and good exposures are consequently rare.

South of the Onny Valley the beds are poorly exposed, but they may be examined in the small valley immediately to the south of Hammondsgreen. Nearer the River Onny, and in the bed of the river itself, exposures are more frequent and yield the characteristic fossils, especially *Broeggerolithus broeggeri*. The latter is accompanied by *Salterolithus caractaci* (Murchison), a species more characteristic of the Middle Harnagian strata, together with *Brongniartella minor subcarinata* Dean, *Onniella avelinei* Bancroft and *Climacograptus antiquus* Hall var. The green mudstones become more arenaceous in the upper part of the zone, where it is thought that they represent what Bancroft called *Horderleyella* Beds or " Burst " after the brachiopod *Horderleyella corrugata* Bancroft (Dean 1958 : 203). The outcrop of the Glenburrell Beds north of the River Onny is poorly exposed but follows the scarp formed by the succeeding Horderley Sandstone as far as the area between Brokenstones and Cwm Head, where it is finally cut out by faults. Some eight miles to the north-east it has been suggested that the *B. broeggeri* Zone may be represented by part of the

so-called "*Glyptocrinus* Flags" in the Chatwall district, indicating a facies change and shallower conditions in that direction (Dean 1960a).

(iv) Horderley Sandstone

This subdivision, perhaps the best known of the Caradoc Series and probably the one Murchison had in mind when he founded the name "Caradoc Sandstone", belongs palaeontologically to the upper half of the Soudleyan Stage and the whole of the Lower Longvillian Substage. Lithologically it commences with green-brown, flaggy sandstones, a transition from the highest Glenburrell Beds, passing upwards into massive, green, brown and purple sandstones which have been quarried extensively for building purposes. The uppermost beds are developed only in the Onny Valley district, where they are rather more flaggy than the underlying strata and show signs of a passage upwards into the Alternata Limestone. Fossils occur predominantly in lenticular bands of sandy limestone. Brachiopods are prolific and have enabled the beds to be divided into four zones, whilst the trinucleid trilobites are of stratigraphical significance, though only locally abundant. *Broeggerolithus soudleyensis* (Bancroft) is fairly common in the Lower Horderley Sandstone, sometimes named *Glyptocrinus* Flags after the abundance of fragments of *Balacrinus* [previously *Glyptocrinus* or *Rhaphanocrinus*] *basalis* (M'Coy), whilst *Broeggerolithus globiceps* (Bancroft) and *B. nicholsoni* (Reed) occur sporadically but characteristically throughout the Middle and Upper Sandstones.

The southernmost exposures of the Horderley Sandstone are found near Sibdon Carwood, where the Lower Sandstones are seen in and near old quarries about 400 yards north-west and west of Castle Farm. The south-easterly dips in this area vary from 18 to 45 degrees according to the position of the rocks relative to the line of The Cwms Fault F3. The higher beds of the Horderley Sandstone are poorly exposed at Sibdon Carwood but crop out at Long Lane where they have been extensively quarried. The rocks there are characterized by *Dalmanella horderleyensis* (Whittington) but *Howellites antiquior* (M'Coy) and *Sowerbyella soudleyensis* Jones are also common. It is at this level in the vicinity of the River Onny that the freestones of the Horderley Sandstone are best developed, and at Long Lane Quarries a total of over 90 feet of mainly massive, green and purple sandstones was at one time exposed. Between Long Lane and the Onny Valley the entire succession of the Horderley Sandstone is exposed in Longville Plantation; at Longville Common; and along the cutting of the old Bishops Castle railway-line by the south bank of the river.

By the north side of the road to Bishops Castle the Lower Horderley Sandstone is seen just south-east of Glenburrell Farm, Horderley; between there and the New House, 600 yards to the south-east, the Middle Sandstones have been quarried on a large scale, and by the west side of New House itself the topmost strata, containing *Bancroftina tyba* (Whittington), are exposed.

Northwards from the Onny Valley massive Middle Sandstones containing Lower Longvillian fossils are found in the old quarry at Briar Edge, south-west of Woolston, and again in the quarry at the western end of Woolston Lane. At both these

localities the strata are almost vertical owing to their proximity to The Cwms Fault F3.

To the north of Woolston exposures are infrequent, but the Horderley Sandstone forms prominent features east of the Brokenstones district, and the Middle Sandstones appear to have been worked in old diggings 1,000 feet due south of Blakemoor. South-east of Cwm Head only Horderley Sandstone débris has been seen, but in the old quarries by the sides of the road about 500 yards south-west of Whittingslow are massive purple and green-brown sandstones with a Lower Longvillian fauna indicating the zone of *Dalmanella indica* and *D. lepta*. The close proximity of the conjectured outcrop of the Alternata Limestone immediately to the east of the quarries suggests a possible overstep of the topmost Horderley Sandstone by the limestone ; if so, this would be in accordance with the break known to occur at the base of the Alternata Limestone farther north in the Caradoc District.

No more solid exposures of Horderley Sandstone are known within the limits of the map, though fragments north-west of Whittingslow suggest that the rock forms the feature there. There is also room for a conjectured outcrop between the Alternata Limestone of the road-section north-east of Crosspipes, near Whittingslow, and the basal beds of the outlier of Llandovery Series at New House, Marshbrook, but no exposures have been found.

(v) Alternata Limestone

This is one of the most useful mapping horizons within the Shropshire Caradoc Series and is marked by the sudden appearance, in vast number, of the brachiopod *Heterorthis alternata* (J. de C. Sowerby). Lithologically the beds comprise dark-green, flaggy siltstones which enclose numerous conspicuous limestone and fine-grained calcareous sandstone lenses made up almost entirely of *H. alternata*, together with the less abundant *Sowerbyella sericea* (J. de C. Sowerby) and *Kjaerina bipartita* (Salter), the last-named being of zonal significance. Higher in the succession the limestone lenses become fewer and there is a gradation into the Lower Cheney Longville Flags. The thickness of the so-called "limestone" in the vicinity of the River Onny is usually of the order of 60 feet.

The Alternata Limestone may be examined in the sides of Longville Lane, 465 yards north-west of the "Earthwork" at Cheney Longville, and also in the cutting of the old Bishops Castle railway by the south bank of the River Onny, 150 yards south of New House. South of Longville Lane the outcrop is obscured by Drift, but north of the River Onny it is exposed to the east of Briar Edge, and in the lane section at Woolston. In this vicinity the beds are almost vertical owing to the nearby Cwms Fault F3, and sometimes form a slight feature. From Woolston the narrow outcrop of the Alternata Limestone extends north-north-eastwards, displaced at intervals by small faults, to the neighbourhood of Whittingslow. Dark-green flaggy siltstones are exposed in the east side of the road leading south from Whittingslow, about 100 yards from the road junction, and are believed to belong to this horizon. By the east side of the Horderley—Marshbrook road, 433 yards north-east of Crosspipes, strata of the Alternata Limestone are exposed. *H. alternata* is not

common at this point, flaggy siltstones predominating in place of the more usual limestone lenses, but *Broeggerolithus longiceps* (Bancroft) occurs. Similar rocks are exposed in the west side of the same road 133 yards farther north-east.

Beyond the north-eastern limit of the present map the base of the Alternata Limestone is known to rest disconformably on earlier strata. It has been shown that at Soudley and Chatwall the underlying rocks belong respectively to the Upper Soudleyan Stage and to an attenuated middle portion of the Lower Longvillian Substage (Dean 1960a).

(vi) Cheney Longville Flags

The strata of this subdivision follow the Alternata Limestone conformably and it has been found possible to map an upper and a lower group of beds. The line separating the two is founded on the palaeontological demarcation between the Upper Longvillian Substage and the Marshbrookian Stage, but in general it can also be said that whilst the Lower Cheney Longville Flags comprise dark-green flaggy siltstones with only occasional shelly bands, the Upper Cheney Longville Flags are lighter and browner in colour with more abundant fossiliferous horizons, the topmost strata including also subsidiary mudstones which indicate a transition to the succeeding Acton Scott Beds. The whole succession is reasonably well exposed in the sides of Longville Lane, west of Cheney Longville, but southwards from this road they are obscured by Drift until they disappear under the unconformable Silurian rocks north-east of Sibdon Carwood.

Near the south bank of the River Onny the upper part of the Lower Flags is well exposed at the north-eastern end of Burrells Coppice, and the Upper Flags crop out along the river bank to the east. Just north of the River Onny, exposures through most of the subdivision are to be found by the north side of the Bishops Castle road. Farther north from the Onny Valley the outcrop of the Cheney Longville Flags extends in a strip about half a mile wide to Woolston, where the Lower Flags are affected by The Cwms Fault F₃. To the north of Woolston and west of the line of F₃ the outcrop is narrow, owing to the greater dip of the strata there ; few outcrops of the Lower Flags are seen, but the Upper Flags are well exposed at the old quarry half a mile east of Cwm Head ; in the sunken track leading north-east from Whittingslow to Marshbrook ; and at Marshbrook itself in the road-sections immediately north and west of the village. North of Woolston and east of the line of F₃ the Lower Flags do not crop out but the Upper Flags, dipping gently south-east, form a tract about half a mile wide running roughly north-east. The rocks may be seen at several points around Bushmoor Coppice and in the well-known section through Marsh Wood, south of Marshbrook, which is the type-locality of the Marshbrookian Stage. Just to the north of Marsh Wood the rocks are folded gently to form a small anticline, with axis running north-east, which accounts for the small outcrop of Acton Scott Beds near Rose Villa, Marshbrook (see Pl. 2). The elevated, partially wooded ground immediately west of Marshbrook is composed largely of Cheney Longville Flags. Lower Flags are well exposed in the north bank of the stream 470 yards at 225° T from Marshbrook Station, where they dip eastwards

at about 37 degrees and have yielded *Strophomena grandis* (J. de C. Sowerby) and numerous *Kjaerina*, including *K. cf. typa* Bancroft. To the west the beds are apparently faulted against Acton Scott Beds, though the contact is not visible, whilst to the east the succession passes upwards into the Upper Cheney Longville Flags.

In the vicinity of the hamlet known as The Corner the outcrop of the Cheney Longville Flags is covered by Drift, but the Bancroft Collection at the British Museum (Nat. Hist.) contains specimens obtained from a nearby well-digging. The fossils indicate the topmost zone, that of *Onniella reuschi*, of the Upper Flags and include *Broeggerolithus cf. transiens* (Bancroft) with *Kjerulfina polycyma* Bancroft (Dean 1960 : 126). The supposed position of the well is shown on the accompanying map (Pl. 2).

(vii) Acton Scott Beds

The term is used here in a broad sense to include all the strata belonging to the Actonian Stage and cropping out at, and immediately adjacent to, the Onny Valley. Acton Scott Beds as employed by Bancroft (1933) included all the Actonian together with the lower two-thirds of the Onnian, and this usage is thought to be best rejected. It has been pointed out already (Dean 1958 : 211-12) that the arenaceous strata cropping out at Acton Scott, to which the name Acton Scott Beds most obviously applies, represent only the middle portion of the Actonian Stage at its type-section in the Onny Valley, but for mapping purposes it is preferable to extend the limits of the term rather than introduce a new stratigraphical name.

The lowest beds crop out along the Onny Valley at Jack Slither, 80 yards west of the junction of the river with the stream known as Batch Gutter, the total thickness being of the order of 200 feet. The rocks themselves comprise grey, often micaceous mudstones with occasional shales and nodular or flaggy limestone bands. Many horizons are fairly fossiliferous, containing trilobites (*Calyptaulax*, *Chasmops* and *Platylichas*), brachiopods (*Cryptothyris* and *Onniella*), gastropods, ostracods and occasional graptolites. Over the greater part of the present map exposures are uncommon, and in the south are limited to the vicinity of the Onny Valley where the rocks crop out by the north side of the Bishops Castle road about half a mile west-south-west of Wistanstow Church, and again, along the small valley of Batch Gutter, about half a mile west of Wistanstow. North of Batch Gutter the outcrop extends only a short distance before being cut by an almost north-south fault which moves it dextrally so that it is presumed to lie beneath the Drift of the Wistanstow district.

Just north-east of the present map the Acton Scott Beds are exposed at several points around the village of Acton Scott, where they form a capping to the high ground east of the valley in which Marshbrook stands. They overlies higher members of the Cheney Longville Flags, the outcrop of which is probably separated by a north-north-westerly fault from the earlier described outcrops of the Upper Cheney Longville Flags at and near Marsh Wood, on the west side of the Marshbrook valley.

As already noted, a small outcrop of Acton Scott Beds occurs just west of Rose Villa, Marshbrook, but the rocks, which yielded the type-specimens of the brachiopod *Reuschella semiglobata* Bancroft, are poorly exposed.

A small, isolated outcrop of Acton Scott Beds occurs just north-west of the fork in the stream situated about 530 yards at 255° T from Marshbrook Station. The exposure, in the bed and banks of the stream, comprises only a few feet of rock, mainly orange-weathering, grey, flaggy siltstones with some grey shaly mudstones. The fauna is sparse but includes *Hedstroemina* and *Onniella* of Actonian type. The beds dip just north of east at about 20 degrees, and although their structural relationships are obscured by Alluvium, they are evidently faulted against Lower Cheney Longville Flags which crop out farther downstream. In appearance these Actonian strata are reminiscent of some of those found in the vicinity of Hatton, two miles to the east, and probably represent a westward extension of the outcrop near Rose Villa, Marshbrook. The beds are shown on the map as being overlain by the Silurian rocks of the New House Outlier, but the ground is badly exposed and the junction of the two has not been seen.

(viii) *Onnia* Beds

Although the remains of *Broeggerolithus* and *Tretaspis* are rarely found in the Acton Scott Beds, other trinucleid trilobites appear in great abundance at the base of the remaining subdivision of the Caradoc Series, strata to which the name *Onnia* Beds, after the predominant genus present, has been given (Dean 1958 : 213). The strata are divided into three successive zones of *Onnia*? *cobboldi* (Bancroft), *Onnia gracilis* (Bancroft) and *O. superba* (Bancroft), the respective thicknesses being about 45, 60 and 70 feet. Lithologically the rocks represent a transition from the Acton Scott Beds but are more argillaceous. Strata of the topmost zone form the lower part of the well-known "Onny Section", the small cliff in the north bank of the river 720 yards west-south-west of Wistanstow Church, where they are overlain unconformably by the Purple Shales of the Upper Llandovery. At that point the *Onnia* Beds comprise mudstones which weather orange-brown but appear grey when unweathered in the river-bed. It is now known that these, the highest strata of the type Caradoc Series, are not younger than the zone of *Dicranograptus clingani* (Dean 1958 : 230). Their outcrop disappears beneath the Drift of the area immediately north of the Onny Valley, but Salter & Aveline's record (1854 : 69) of "*Trinucleus* Shales" at Henley, one mile south of Acton Scott, suggests an extension northwards. In his manuscript map of part of south Shropshire Bancroft did, in fact, show what are now *Onnia* Beds both at Henley and near Hatton Wood, east of Acton Scott, but such outcrops are probably of only limited occurrence, and elsewhere in the Caradoc district are overstepped by the base of the Silurian.

The Acton Scott Beds and *Onnia* Beds contain a fauna which includes many Scandinavian elements, and these have enabled the two subdivisions to be correlated with Stage 4bδ of southern Norway and parts of Sweden.

V SILURIAN ROCKS

As long ago as 1854 Salter & Aveline recognized that the beds between the "Caradoc Sandstone" and the Wenlock Shales could be subdivided into three parts. Their succession, now assigned to the Upper Llandovery Series, is as follows :

- { Purple Shales
- Pentamerus* Limestone
- { Coarse grits of Church Preen, Kenley, etc.

The nomenclature was later slightly modified by Whittard (1928) to comprise Purple Shales, *Pentamerus* Beds and Arenaceous Beds. Since then the Geological Survey (Pocock *et al.* 1938 : 106) has employed the succession :

- { Hughley Shales
- Pentamerus* Beds
- { Kenley Grits.

These terms are of local application, and in the present work Whittard's more general stratigraphical names are used. His method of separating the Silurian rocks geographically rather than merely stratigraphically has been found most convenient and three outcrops are now discussed, the Main Outcrop, the Longmynd Margin Outcrop and the faulted outliers of Cwm Head and Marshbrook, the two last being considered together.

(i) The Main Outcrop

The lowest Llandovery strata found are the *Pentamerus* Beds, containing abundant *Pentamerus oblongus* (J. de C. Sowerby). A little to the north-east of the present map they lie unconformably on mudstones of the Actonian Stage in Ticklerton Brook, north-west of the village of Ticklerton. Their outcrop narrows to the south-west owing to overlap by the succeeding Purple Shales, and at the River Onny the latter beds rest unconformably on the topmost strata, *Onnia* Beds, of the Caradoc Series. Between Ticklerton and the Onny the Caradoc/Llandovery boundary is obscured by thick Drift deposits.

South-west of the Onny Valley the Purple Shales are overstepped by the Wenlock Shales ; the latter can be seen, dipping gently east-south-eastwards, at Sibdon Pool, Sibdon Carwood, where they probably overlie part of the Horderley Sandstone of the Caradoc Series.

In the vicinity of Aston-on-Clun the Silurian rocks are covered by Drift and Alluvium of the Clun Valley, but Wenlock Shales, which must rest on strata of Costonian and Harnagian age, have been proved in a boring for water at the village itself (Whittard *in* Dean 1958 : 226). The high ground formed by the Costonian rocks of the Coston district is probably bordered on the east by Wenlock Shales, but a few fossils in the Bancroft Collection at the British Museum (Natural History) indicate the presence of a small outlier, not now visible, of arenaceous Purple Shales just to the south-east of The Hollies farm. They include *Mendacella*, *Pentamerus* and *Plectodonta*, and the rocks contain some quartz-pebbles such as are common in the subjacent Coston Beds and Smeathen Wood Beds (see earlier).

(ii) The Longmynd Margin Outcrop

This includes all Silurian strata found immediately west of the Church Stretton Fault F1, and extends at least as far south as the Clunbury district. Although Llandovery beds are known from the south-eastern border of The Longmynd, where they have been mapped by Whittard (1932), the lowest strata found along the western side of F1 within the limits of the present map are the Wenlock Shales, which form part of the low-lying ground between The Longmynd and the ridge of high ground running from Marshbrook to Horderley. In the old quarry at Pillocksgreen, near Cwm Head, the beds are seen to be shattered and near vertical owing to the proximity of the Church Stretton Fault. Grey shales dipping south-eastwards are exposed in the so-called " Sand Pit " on the north-western side of the stream opposite Brokenstones (see Text-fig. 2), where they have yielded a fauna containing *Calymene* cf. *nodulosa* Shirley and *Monograptus priodon* (Bronn). The shale outcrop may be traced south-westwards in the direction of Horderley, where a higher, more calcareous development appears and forms the feature known as The Bank, to the south-west of the Red Lion.

South of the River Onny strongly-cleaved, dark grey-green mudstones crop out to the south-west of Wart Hill at Laplow Quarries and Grist House quarry, in the vicinity of the hamlet of Round Oak. The former locality has yielded only *Slava interrupta* (J. de C. Sowerby), but at the latter *Dayia navicula* (J. de C. Sowerby) is abundant and probably indicates an Upper Ludlow age.

An interesting section is exposed near Hopesay, in the disused quarry 250 feet north of the Fish Pond. The strata there are much disturbed by the nearby Church Stretton Fault F1, but dip generally north-westwards, away from the fault-line. The lowest beds, fissile grey shales a few feet thick, are seen at the eastern end of the quarry face where they have yielded numerous graptolites, many poorly preserved. The better specimens have been identified by Dr. I. Strachan as *Monograptus dubius* (Suess), *M. dubius* var., *M. uncinatus* Tullberg, *M.* cf. *uncinatus* and *M.* cf. *tumescens* Wood; in his opinion the assemblage is probably indicative of the *Monograptus tumescens* Zone of the Lower Ludlow, that is to say, equivalent to the Upper Elton Beds of the type succession in the Ludlow district (Holland *et al* 1959). The shales are overlain, apparently conformably, by thin and massively-bedded limestones which have yielded a relatively small number of fossils, including *Dalmanites* cf. *myops* (König), *Leptaena rhomboidalis* (Wahlenberg) and, most important, rare *Conchidium knighti* (J. de C. Sowerby). The limestones therefore probably represent the lateral equivalent of the Aymestry Limestone, well developed along View Edge, near Craven Arms, but not previously known from the Hopesay district, two-and-a-half miles to the north-west.

Between Hopesay and Aston-on-Clun the strata immediately to the east and west of the Church Stretton Fault are covered by Drift and Alluvium, and on the north side of the River Clun good exposures are not available until Oaker Quarry, about one mile west of Aston, is reached. There the rocks, comprising about 80 feet of well-bedded, dark grey-green mudstones and impure limestones, dip south-east at 25 degrees; the fauna includes abundant *Protochonetes ludloviensis* Muir-Wood

suggesting an horizon high in the Ludlow Series. *P. ludloviensis* is also found abundantly in the small, disused quarry 800 yards almost due north of Coston Farm, where the beds are shattered and the line of the Church Stretton Fault runs about 100 yards to the east.

As far as can be ascertained, the whole of Clunbury Hill is made up of Upper Ludlow Beds containing abundant *P. ludloviensis*. In the absence of marker bands it has not proved possible to map minor structures satisfactorily, but the general picture is of a syncline, the northern end of which meets the Church Stretton Fault at an acute angle (see Pl. 1). The fauna of the local strata with *Protochonetes* is best examined in the disused quarry 1,000 yards north-east of St. Swithun's Church, Clunbury, where the rocks dip south-eastwards into the hill at about 32 degrees. From the position of this quarry in the vicinity of Shelveswell Cottage, Clunbury, it has been termed Shelveswell Quarry by Whittard (1953 : 233), but this name is not in general use locally, where it is known as Hill End Quarry. At this point fossils are abundant and include numerous *P. ludloviensis*, *Resserella* sp., *Dalmanites* sp. and orthocone nautiloids. Lithologically the beds comprise dark-green mudstones with thin limestone bands ; the rocks have been much affected by faulting and the mudstones are often slickensided.

(iii) The Cwm Head and Marshbrook Outliers

These two masses of Silurian rocks are separated from The Longmynd Margin outcrop by faults of the Church Stretton system ; both were referred to by Whittard (1932 : 863-65) but, owing to the paucity of exposures near Cwm Head, only a map of the Marshbrook Outlier was published by him.

The Marshbrook Outlier is relatively simple in structure, consisting of an elongated outcrop of Llandovery strata extending north-east for about one mile, bounded on the west by the Church Stretton Fault F₁, and on the east by the unconformity at the base of the Llandovery Series. In the stream-section to the south of New House conglomerates are visible dipping north-west at 35 degrees, followed stratigraphically by mudstones containing *Pentamerus oblongus*. Whittard (1932 : 864) has shown that the conglomerates belong to the arenaceous facies of the *Pentamerus* Beds. The Llandovery strata of this neighbourhood rest unconformably on various members of the Caradoc Series ranging from, probably, Middle or Upper Horderley Sandstone to Lower Cheney Longville Flags and Acton Scott Beds, all of which have a general south-easterly dip (see Pl. 2).

The Cwm Head Outlier is a more complex structure, and the Silurian strata form outcrops which are completely bounded by faults. Llandovery rocks, comprising layers of hard, blue limestone, veined with calcite and containing *Pentamerus oblongus*, together with micaceous shales are known to crop out near the western end of the stream-section running west-south-west through Blakemoor Wood, south-west of Cwm Head, but exposures are poor and the underlying beds are not known, though they are provisionally shown as one with the *Pentamerus* Beds on the accompanying map (see Text-fig. 2). The strata immediately to the east and north-east are respectively Lower Ludlow Shales and Wenlock Shales, and the junctions of all three are believed to be faulted.

North of Blakemoor Wood, and extending to a point midway between Pillocks-green and Crosspipes, are outcrops of both Wenlock and Ludlow strata. The former includes a limestone development, here given the local name of CWM HEAD LIMESTONE as its equivalence to the Wenlock Limestone of Wenlock Edge is not yet proved. This limestone, which has been quarried locally, forms a marked ridge running north-north-east through Cwm Head farm, near which it is "stepped" slightly by a small transverse fault. The Wenlock Shales give rise to a strip of marshy ground to the north-west of the ridge of Cwm Head Limestone, and few solid exposures are available. On the south-eastern side of the limestone ridge the Lower Ludlow Shales floor an area of low ground and are exposed in the stream-section 100 feet south-east of Cwm Head farm, where they have yielded a graptolite fauna indicative of the *Monograptus nilssoni* Zone (Whittard 1932 : 865).

According to Whittard (1952 : 171) there is a "surprisingly abrupt" facies change across the Church Stretton fault-system, the Wenlock Series of the Cwm Head district being described as intermediate between the true graptolitic and the shelly facies, and brought into juxtaposition with the graptolitic development of the Longmynd Margin Outcrop. Such a statement implies the existence of a physiographic feature along the line of the fault-system, and, as Whittard (1952 : 171) has pointed out, there is no indication of such a feature having existed during Upper Llandovery times. The two topmost graptolite zones of the Llandovery Series, *Monograptus griestonensis* and *Monograptus crenulatus* successively, are, however, absent, as is the lowest part of the Wenlock Series (Whittard 1952 : 167-68) and the possibility exists of there having been contemporaneous movement along the fault-system.

Owing to the paucity of exposures it has not been possible to compare in detail the Wenlock Shales of the Cwm Head district with the equivalent beds on the western side of the Church Stretton Fault, but it is difficult to accept any fundamental difference between the two groups. The higher, calcareous beds to the west of F1 near Horderley are poorly known, but may be the lateral equivalent of the Cwm Head Limestone. Although Whittard has described the Wenlock Series within the fault-system as being of an intermediate graptolitic-shelly facies, the fauna of the lower Wenlock beds to the west of F1 includes numbers of both graptolites and trilobites. While conceding that the Cwm Head Limestone differs from the Wenlock Limestone of the type-area and shows no development of "reefs", the idea of a change in lithology across the line of F1 is less acceptable. Whittard (1953 : 247) has stated that the "Wenlock Limestone" of Cwm Head, that is to say the Cwm Head Limestone, indicates a facies different from that at the so-called "Sand-Pit", actually a disused quarry, north-west of Brokenstones, but this statement does not, apparently, take into account the probable difference in age of the two deposits. The shales exposed in the "sand pit" contain fairly abundant *Monograptus priodon* (Bronn), a species which, according to Elles & Wood (1918 : 524), does not occur higher than the *Cyrtograptus linnarssoni* Zone, where it is rare. The Cwm Head Limestone underlies Lower Ludlow Shales of the *Monograptus nilssoni* Zone so that, although no definite evidence is yet available, its possible age

is that of the *Monograptus vulgaris* Zone. Thus it seems likely that the deposits are of different age, and that the Wenlock Shales to the west of F1 are followed in the succession by the equivalent of the Cwm Head Limestone, but confirmatory evidence is still lacking.

VI THE UPPER LIMIT OF MURCHISON'S "CARADOC SANDSTONE"

My attention was drawn by Prof. W. F. Whittard to the fact that on the Geological Survey's one-inch map, Old Series, Sheet LXI S.W., a dotted line extends roughly north-eastwards from near the south-western corner of the map. He suggested that this might indicate the top of the "Caradoc Sandstone" as understood by Murchison, and I am indebted to Dr. C. J. Stubblefield for permission to publish the following note, written by him to Prof. Whittard.

"Copies of this map were issued in 1850 and the dotted line represents the boundary between "Caradoc or Middle Silurian" and the Wenlock Shale division of the "Upper Silurian". The first of these units had written across it "SANDSTONES AND CONGLOMERATES WITH FEW BEDS OF SHALE" and the later beds were similarly inscribed across the body of the map "CALCAREOUS GREY SHALES". The 1855 edition, marked "Geological information published January 1855", had introduced into its legend, above the Caradoc or Middle Silurian, a tablet called *Pentamerus* Limestone, and below the Caradoc or Middle Silurian another tablet called *Pentamerus* Conglomerate. Below that came another tablet called Llandeilo Beds or Lower Silurian; this last tablet refers to the beds which in the next map were symbolized b3. The line in question north of Hatton finds itself within the Wenlock Shale outcrop.

"There is a third printing of this map, undated other than Jan. 1855 or before but most certainly after 1855, and on this map symbols are introduced and a new legend. The boundary between Upper Silurian and Lower Silurian is clearly indicated above the Caradoc or Bala Beds and below the Upper Llandovery rock (Mayhill Sandstone). This last map has on the bottom right-hand side an added piece of information "Geologically surveyed by W. T. Aveline and A. C. Ramsay, Local Director".

The present account, based on my own field mapping, is an attempt to reconcile the top of the "Caradoc Sandstone" with the subdivisions of the Ordovician and Silurian rocks recognized today in south Shropshire.

Near the south-western corner of the map the course of the dotted line runs approximately coincident with the base of the Silurian (in its present-day sense) near Long Meadowend, east of Aston-on-Clun, and then cuts the north-western corner of Sibdon Castle. In this neighbourhood it appears to pass through the outcrop of the various members of the Horderley Sandstone group, and then runs about a quarter of a mile east of Long Lane Quarry, which is excavated in Middle Horderley Sandstone. One may reasonably assume that the line was intended to mark the upper limit of such a sandstone. From Long Lane it extends through the outcrop of the Cheney Longville Flags as far as the Onny Valley, where its course intersects the river about 200 yards west of the confluence with Batch Gutter, and

presumably marks the junction of the Cheney Longville Flags (here flaggy siltstones) and the overlying Acton Scott Beds (here grey mudstones). The line extends from the river Onny at the same stratigraphical level, parallel to Batch Gutter, through Leamoor, Cuckold Corner and Botley Moor Wood (probably at about the same horizon, though this is obscured by glacial drift), and intersects the main Ludlow-Shrewsbury road south-east of Marsh Wood, at a point where it crosses the stream from Marshbrook, and where the highest Cheney Longville Flags are exposed in the west bank. Thence the line runs through Acton Scott village just by the south-eastern corner of Acton Scott Hall, and its course here is difficult to correlate with known strata, though it may be an attempt to differentiate the arenaceous facies of the Acton Scott Beds, developed here, from the overlying grey mudstones of both Actonian and Onnian age. North-eastwards from Acton Scott the line runs about one-eighth of a mile south-east of Hatton village, probably at about the conjectured top of the Acton Scott Beds. It then turns farther eastwards to cut the line marking the base of the Silurian strata, and finally slightly more northwards to intersect Ticklerton Brook at a point which probably represents the present-day boundary between the arenaceous *Pentamerus* Beds and the overlying Purple or Hughley Shales. From here the line extends north-eastwards roughly parallel to the base of the Silurian strata, and may represent an attempt to distinguish the upper limit of the Arenaceous Beds. This course is maintained past Wallsbank to just beyond Gilberries, but from here on it runs to Hughley village and climbs progressively higher in the Silurian outcrop, and it is difficult to equate it with any junction such as that, say, between the Hughley Shales and Wenlock Shales.

VII IGNEOUS ROCKS (EXCLUDING URICONIAN)

Igneous rocks, other than those of the Uriconian, are relatively unimportant in the Caradoc district ; they may be discussed under two headings.

(i) *Extrusive rocks.* The first mention of any such igneous rocks was made by Lapworth (*in* Lapworth & Watts 1894 : 320) who described the presence at Acton Scott of what he called " a peculiar igneous rock ", though without giving any details of the locality or rock-type. The record was perpetuated by Cobbold (1900 : 51) who claimed that the high ground at Acton Scott village was caused by the thickening of the Acton Scott Beds due to the intercalation of the igneous rock. Again, no mention was made of places where exposures could be found. As far as I am aware, no outcrops of igneous rock are visible at Acton Scott, and the prominent feature near the village is considered to result from the more resistant, arenaceous facies of the Acton Scott Beds there, compared with the soft grey mudstones of the same age in the Onny Valley.

Undoubted volcanic rocks are to be found in the neighbourhood of Sibdon Carwood, where Whittard (1952 : 162) has recorded the occurrence of a volcanic agglomerate and lava flow of trachybasalt in the " Gravel Pit " situated 2,300 feet west-north-west of St. Michael's Church. The lava flow, about 30 feet thick, can be traced southwards as far as the old diggings 800 feet north-north-east of Oldfield Farm. In another old digging, 80 feet west of that already mentioned, a second lava

flow was seen, but owing to the poorly exposed nature of the ground it proved impossible either to trace it farther or to gauge its thickness accurately. The flows are associated with shales and mudstones of the Smeathen Wood Beds, Harnagian Stage, and indicate slight igneous activity in the early part of the *Diplograptus multident* Zone, an horizon which also contains the Caradoc vulcanicity of the Shelve Inlier in west Shropshire.

The record by Bancroft (1933) of an ash band in the Glenburrell Beds has not yet been confirmed, and so far as is known no other extrusive igneous rocks crop out within the Caradoc District.

(ii) *Intrusive rocks.* The only examples yet known are two dolerite dykes which crop out in the stream-bed immediately to the south of the "Sand Pit" north-west of Brokenstones Plantation (see Text-fig. 2).

The more northerly of the two dykes has been referred to by Whittard (1953 : 247) as an intrusion of spilitic basalt, and the other is of similar type. The trend of the dykes is approximately north-west and they cut Western Longmyndian rocks ; they have not been found to extend into the Eastern Longmyndian rocks, but the neighbourhood is only poorly exposed. The intrusions cannot be definitely dated, other than to state that they are post-Western Longmyndian, but numerous similar intrusions of Pre-Cambrian age are known to cut Western Longmyndian rocks elsewhere in south Shropshire (Cobbold 1900 : 105-106) and may be related.

VIII GEOLOGICAL STRUCTURE

(i) The Church Stretton fault-system

The fractures constituting what is usually known as the Church Stretton fault-system contain a belt of disturbed strata extending in a roughly north-easterly direction. The three dominant fault-lines were first described by Cobbold (1900 ; 1927) from the neighbourhood of Caer Caradoc, near Church Stretton. From west to east they were designated by him as F₁ the Church Stretton Fault, F₂ The Lawley Fault, and F₃ The Cwms-Hoar Edge Fault, and they may conveniently be discussed in this order.

(a) *The Church Stretton Fault F₁.* This structural line has been known for many years and was at one time thought to have a throw of up to 6,000 feet, but more recently Whittard (1932 : 883) has shown that, at one point at least, it has a post-Wenlock downthrow to the west of only 600 feet, though the value may vary elsewhere. The place where this was demonstrated, near New House, west of Marshbrook, is the only one in the southern Caradoc District where similar members of a stratigraphical series are brought into juxtaposition by the fault.

In the southern part of the accompanying map, F₁ is first encountered near Coston where it separates basal Caradoc strata, the Coston Beds, from rocks of the Upper Ludlow Series forming Clunbury Hill immediately to the west. Whittard (1953 : 233) has described the regional dip in this area as being to the east on both sides of the fault, but near F₁ drag effects have produced a westerly dip immediately to both sides of the fault-line.

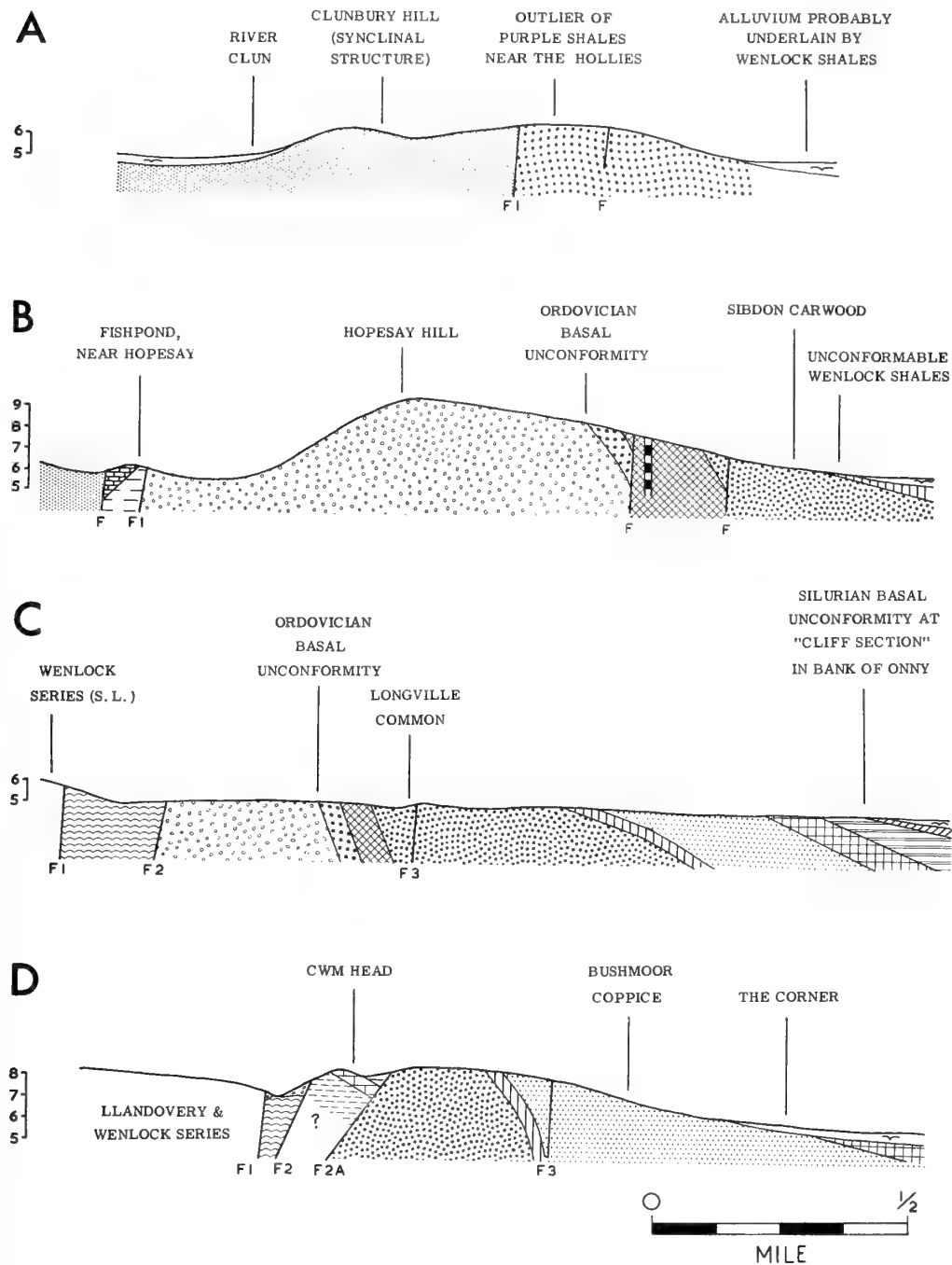


FIG. 3

Although covered by Alluvium of the River Clun near Aston-on-Clun the general line of F1 is shown clearly in the topography, and separates the prominent features of Burrow (Upper Ludlow Series and, perhaps, younger strata) and Hopesay Hill (Western Longmyndian). It continues northwards through the villages of Hopesay and Round Oak, but beyond the area of Wart Hill changes direction slightly, showing a north-easterly trend as it passes near Horderley and along the line of the Horderley-Marshbrook valley, where Wenlock beds are brought into contact with Eastern and Western Longmyndian (see Pl. 2). The fault-line passes almost directly beneath Crosspipes, immediately to the north of which it forms the western boundary of the Marshbrook Outlier of Llandovery rocks, and continues in the general direction of Little Stretton and Ragleth Hill.

(b) *The Lawley Fault F2*. The first detailed account was that of Cobbold (1927 : 565) who described the outcrop of the fault near Comley as being sinuous and convex to the east on the higher ground, indicating a westerly hade calculated to be about 45 degrees. On the eastern slopes of Caer Caradoc the fault brings Uriconian over Cambrian rocks and is a compressional or reversed fault ; from the behaviour of the Lower Cambrian Quartzite on Little Caradoc, Cobbold suggested F2 to be the fractured septum of a large fold.

In the area mapped, the southernmost extension of F2 is found immediately south of Wart Hill, where the fault-line is apparently truncated by that of F1. In this part of the map F2 forms the eastern boundary of the three Uriconian outcrops already described, and to the north, near Horderley, is important in that it separates the Eastern Longmyndian outcrop from that of the Western Longmyndian immediately to the east. At Wart Hill the conjectured outcrop of F2 suggests that it is a thrustplane with a hade, at this point, of about 60 degrees to the north-west. The nearby Uriconian outcrop of Palace Coppice is also believed to have undergone thrusting from the north-west, as may be indicated by the sinuous line of F2 which forms its eastern boundary. The western boundary of the Uriconian at Wart Hill and Palace Coppice is also thought to be faulted, the line of faulting being truncated by both F1 and F2.

Northwards from Palace Coppice the outcrop of F2 is at first gently curved and then almost straight, the hade apparently being less than at Wart Hill. North-east of Horderley, between Brokenstones Plantation and Pillocksgreen (see Text-fig. 2), the main line of F2 is interpreted as being that which separates the Pre-Cambrian rocks of the valley from the Ordovician and Silurian strata of the Brokenstones-Cwm Head area. An important tensional fault-line forms the eastern boundary of the Cwm Head Outlier of Silurian rocks ; it is associated with part of the general line of F2 and, as a matter of convenience, is called F2A. To the north-east of Pillocksgreen the outcrops of both F2 and F2A are truncated by F1.

A smaller fault associated with F2 separates the Coston Beds of Brokenstones Plantation, with a north-westerly strike, from the area immediately to the south-east, where the strike is north-easterly.

(c) *The Cwms-Hoar Edge Fault F3*. In the vicinity of Caer Caradoc, where the fault was first described, its outcrop, according to Cobbold (1927 : 565), is almost

straight and the fault-plane nearly vertical. Cobbold described it as a septal fault, with gently inclined strata to the east being turned-up vertically, or even reversed, at the fault-line. Earlier he (1900) had written of F₃ as a line separating two regions of high and low dips, to the west and east respectively of the fault, and this conception of the structure has been found to hold good for the area to the south of Caer Caradoc and the other Church Stretton Hills.

The steeply-dipping strata to the west of F₃ often stand out as a pronounced feature in the field, particularly when the massive sandstones of the Caradoc Series are involved. In the south of the map, F₃ can be traced near Sibdon Carwood and Long Lane, where it affects strata of Upper Soudleyan age, the Lower Horderley Sandstone, but by the time the Onny Valley is intersected the disturbed rocks are those of early Lower Longvillian age, the lowest Middle Horderley Sandstone.

North of the Onny the fault-line swings slightly to the north-east and cuts the outcrop of the Alternata Limestone, which is found to be vertical at, and just south of, Woolston. Towards Marshbrook still higher horizons are affected, and at the old quarry north-north-west of Bushmoor Coppice nearly vertical *Dalmanella unguis* Beds of the Upper Cheney Longville Flags, middle Marshbrookian Stage, are seen and form a marked ridge. In the sunken track between Whittingslow and Marshbrook F₃ cuts the *Dalmanella watti* Beds, the lowest subdivision of the Marshbrookian, which are visible on either side of the fault-line. As the thickness of the *D. watti* Beds in this neighbourhood is probably less than 100 feet, the throw of F₃ here must be relatively small. Still farther north F₃ cuts strata of Actonian age west of Rose Villa, Marshbrook, runs just to the east of Marshbrook station, and continues along the eastern margin of Ragleth Hill, passing into the Comley area between Helmeth and Hope Bowdler Hill.

(ii) Transverse faults

Along the belt of ground enclosed by the longitudinal faults of the Church Stretton system, several faults with an approximately east-west trend have been mapped. Those which run between F₂ and F₃ are of relatively small throw, and generally displace the outcrops of the Ordovician rocks sinistrally; it has not proved possible to trace them farther east than F₃.

Faults with a similar trend are found within the complex of the Brokenstones-Cwm Head district (see Text-fig. 2) and these, too, are of small displacement; like the other transverse fractures they end at the line of F₂. It may be noted that Cobbold (1927: 566) described a set of similar transverse faults from the area between F₂ and F₃ near Comley.

(iii) Other faults

To the west of Sibdon Carwood runs an important fault, here termed the Sibdon Cottage Fault, with a roughly north-south trend. With downthrow to the east it is responsible for the vertical position of the Smeathen Wood Beds and associated lava flows near Oldfield (see p. 287), and near Sibdon Cottage it cuts out the Coston Beds

completely. To the north it passes through Hammondsgreen, where Smeathen Wood Beds abut against Western Longmyndian rocks, and at Palace Coppice it joins, and is truncated by, the line of F2. Its southern extension is masked by Drift deposits north-east of Aston-on-Clun, but the available information on the Wenlock Shales of the district does not suggest that the Silurian strata are much affected, if at all.

In the vicinity of Woolston is another north-south fault, with downthrow to the west. Owing to the cover of Drift it has not been possible to measure its throw or to map its extent with any degree of certainty, but it is believed to run southwards at least as far as Wistanstow where it may possibly cut the Silurian unconformity, as shown on the Geological Survey's one-inch map of 1855.

The existence of a fault running just west of north must be postulated to extend along the valley separating Marshbrook and Marsh Wood from the high ground around Acton Scott. High Marshbrookian strata to the west of the fault are brought against lower Marshbrookian beds to the east, and the throw is estimated to be approximately 150 feet. To the west of Marshbrook the faulted relationship of the Acton Scott Beds south of New House to adjacent strata has already been noted. The rocks in this neighbourhood are poorly exposed, and it is not clear whether the faulting involves the Silurian as well as the Ordovician rocks.

Other small faults occur within the area covered by the accompanying maps, some of them, in particular, affecting the outcrop of the Coston Beds; they are probably of minor importance, and the fact that they can be mapped is primarily a consequence of the conspicuous feature formed by the basal Ordovician strata.

(iv) Age of the faulting

The line of what he termed the "Church Stretton Disturbance" was described by Jones (1927 : 8-20) as separating contrasting developments of Lower Palaeozoic rocks, and marking the boundary between a yielding and a rigid area. He pointed out that in Pembrokeshire large thicknesses of Lower Palaeozoic strata, including Cambrian, are found only on the north side of the coal-field, and this suggests that the line of the "disturbance" was already in existence by Cambrian times. It is known that in Shropshire the Pre-Cambrian rocks had suffered at least two periods of deformation prior to the Cambrian, and it appears probable that the oldest structural line of the Church Stretton fault-system, now considered to be F2, was established at least between Western Longmyndian and Cambrian times, and probably earlier, perhaps between the Eastern and Western Longmyndian.

In the southern Caradoc district extensive movements are believed to have taken place towards the end of the Ordovician, some time after the zone of *Dicranograptus clingani*, when compressional forces caused recurrent thrusting along the line of F2. It has been suggested by Whittard (1952 : 186) that F3 may be a tear-fault, and the present mapping tends to bear out this conclusion, the strip of ground between the lines of F2 and F3 being interpreted as a zone of shearing. In addition to displacing the outcrop of *Alternata* Limestone sinistrally, F3, which has an extremely small throw, is accompanied by several complementary shears, the east-west members

of which are the more prominent and make an angle of 50 to 55 degrees with the line of F₃.

According to Cobbold (1927 : 566) neither F₂ nor F₃ is known to affect Silurian strata, but such a claim is difficult to confirm, at least south of the Comley district. The junction of F₃ with the Silurian unconformity in the south of the present map is covered by Drift, but there is no sign of the ridge of vertical strata that one so often associates with F₃, and it is unlikely that the fault-line does, in fact, affect the unconformity. In the Brokenstones district, however, Silurian rocks as high as the Lower Ludlow Shales are involved in tensional movements along the line of F₂A, and it is likely that posthumous movement took place along the general structural line of F₂, perhaps only a short time prior to the formation of F₁.

With reference to the age of F₁, Cobbold (1927 : 572) suggested that this great tensional fault was formed after the deposition of the "Silurian, Devonian (Old Red Sandstone), Carboniferous, and possibly later deposits", but in the southern Caradoc district it can only be stated definitely that movement has taken place along F₂A since Lower Ludlow times, and that F₁, the line of which truncates F₂A, must therefore be still later in age, at least post-Upper Ludlow. Farther north it has been shown by the Geological Survey (Pocock *et al.* 1938 : 173) that the extension of the Church Stretton Fault, known as the Brockton Fault, underwent movement at least as late as the Trias, for it separates Lower Mottled Sandstone from Keele Beds near Donneville and Wellington.

Important though the Church Stretton Fault System is in south Shropshire, of probably even greater significance is the Linley-Pontesford Fault System, occupying an analogous position along the western margin of The Longmynd. The Ordovician strata immediately east of this structural line, represented by only part of the Caradoc Series in the Pontesford district, are identical in both lithology and fauna with those of the Caradoc district (Dean & Dineley 1961), but are separated by the fault-system from the radically different Ordovician succession of the Shelve Inlier, a short distance farther west. Similarly, the "Wenlock Limestone" of Cwm Head probably crosses the line of F₁, whilst the "Aymestry Limestone" certainly does so, as shown by its outcrop near Hopesay. Jones (1927 : 10) has described the Church Stretton Disturbance as marking the boundary between what he called a yielding and a rigid area, that is to say between two fundamentally different areas of sedimentation. At the present time this concept still holds good in a general sense, but it may be more appropriate to substitute the Linley-Pontesford Fault System for that of Church Stretton, at least as far as the Ordovician rocks are concerned. The important movements producing the tear-fault pattern between F₂ and F₃ are paralleled in the Shelve Inlier of west Shropshire; there, tear-faulting occurring between the lower Caradoc Series and the Upper Llandovery Series has been referred by Whittard (1952 : 186) to the Taconian Orogeny, with some posthumous movements displacing the unconformable Llandovery strata.

The north-south fault through Oldfield and Hammondsgreen, the Sibdon Cottage Fault, is truncated to the north by F₂, and to the south disappears beneath the glacial Drift. Its age is thus difficult to decide, but it may be associated with the

formation of F₃ and its contemporaneous subsidiary structures. Similarly it is difficult to determine the age of the faults near Woolston and between Marshbrook and Acton Scott as their junction with the Silurian unconformity is not exposed.

(v) Folding

This is the least conspicuous of the structural features of the southern Caradoc district. Mention has already been made of the folded Eastern Longmyndian strata overlain by the Western Longmyndian near Brokenstones, and also of the drag-effects associated with, and found to either side of, the line of F₁ near Coston and Clunbury, and giving rise to the anticlinal structure of the Coston Beds in the south of the Coston district. In addition, the outcrop of the Alternata Limestone between Crosspipes and Marshbrook suggests that the Caradoc strata had been slightly folded prior to the deposition of the unconformable Llandovery Series of the Marshbrook Outlier, the rocks of which rest on more than one horizon of the Caradoc Series. There is also a minor synclinal structure, with north-easterly axis, between Marsh Wood and the line of F₃ near Marshbrook, which accounts for the outcrop of Acton Scott Beds poorly exposed to the west of Rose Villa.

(vi) Unconformities

Those found within the limits of the present map, and also in adjacent parts of the Caradoc district, are listed below ; they give no indication of the geological history of the region in the post-Longmyndian, pre-Caradoc Series period.

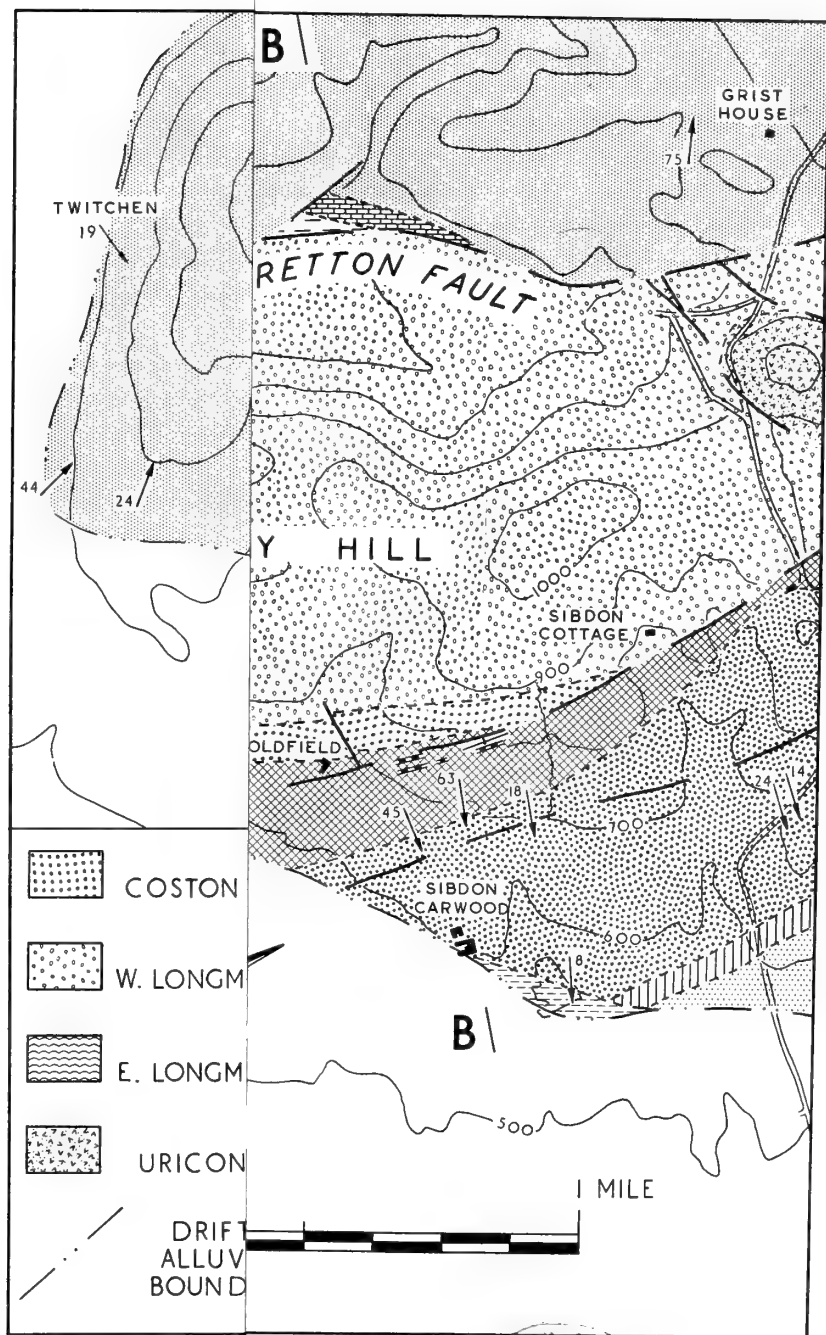
- a. The base of the Western Longmyndian lies unconformably on folded Eastern Longmyndian shales in the neighbourhood of Brokenstones.
- b. The base of the Caradoc Series is diachronous and unconformable throughout the whole of the Caradoc district, resting on various members of the Pre-Cambrian rocks.
- c. In the Onny Valley the Alternata Limestone follows the Horderley Sandstone with apparent conformity, though there is a slight discrepancy of dip. At Soudley, however, the former stratum rests disconformably on Soudley Sandstone of Upper Soudleyan age, whilst at Chatwall the position is even more complex. There the Chatwall Sandstone represents only the middle part of the Lower Longvillian Substage and is separated by stratal breaks from the underlying Chatwall Flags, Soudleyan Stage, and the overlying Alternata Limestone.
- d. The most marked unconformity is that below the Silurian rocks which rest, with overstep, on strata ranging from Uriconian at the Cardington Hills to topmost Caradoc Series in the Onny Valley.
- e. The two highest graptolite zones of the Llandovery Series are missing, and the beds are overstepped by the often incomplete Wenlock Series.

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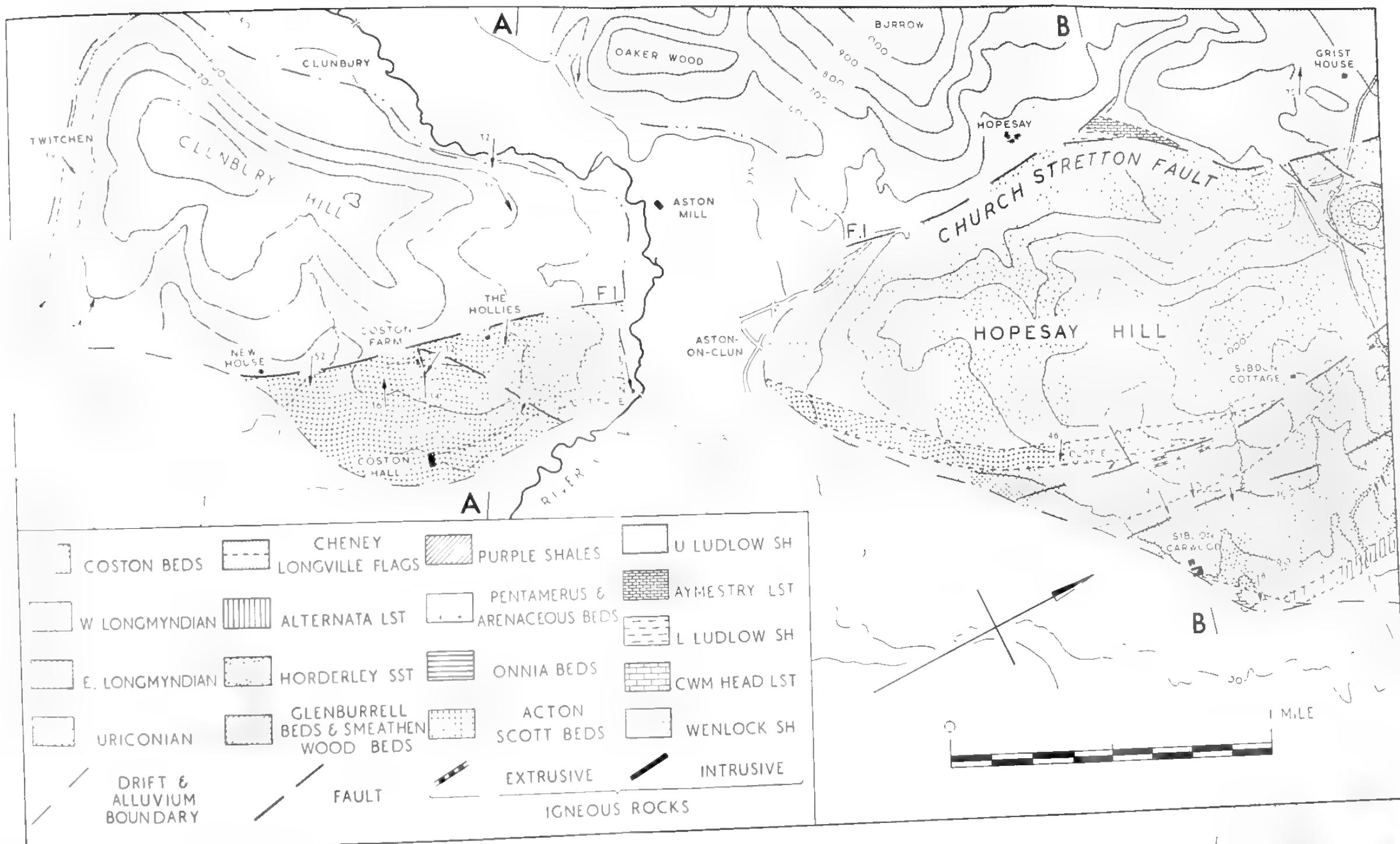
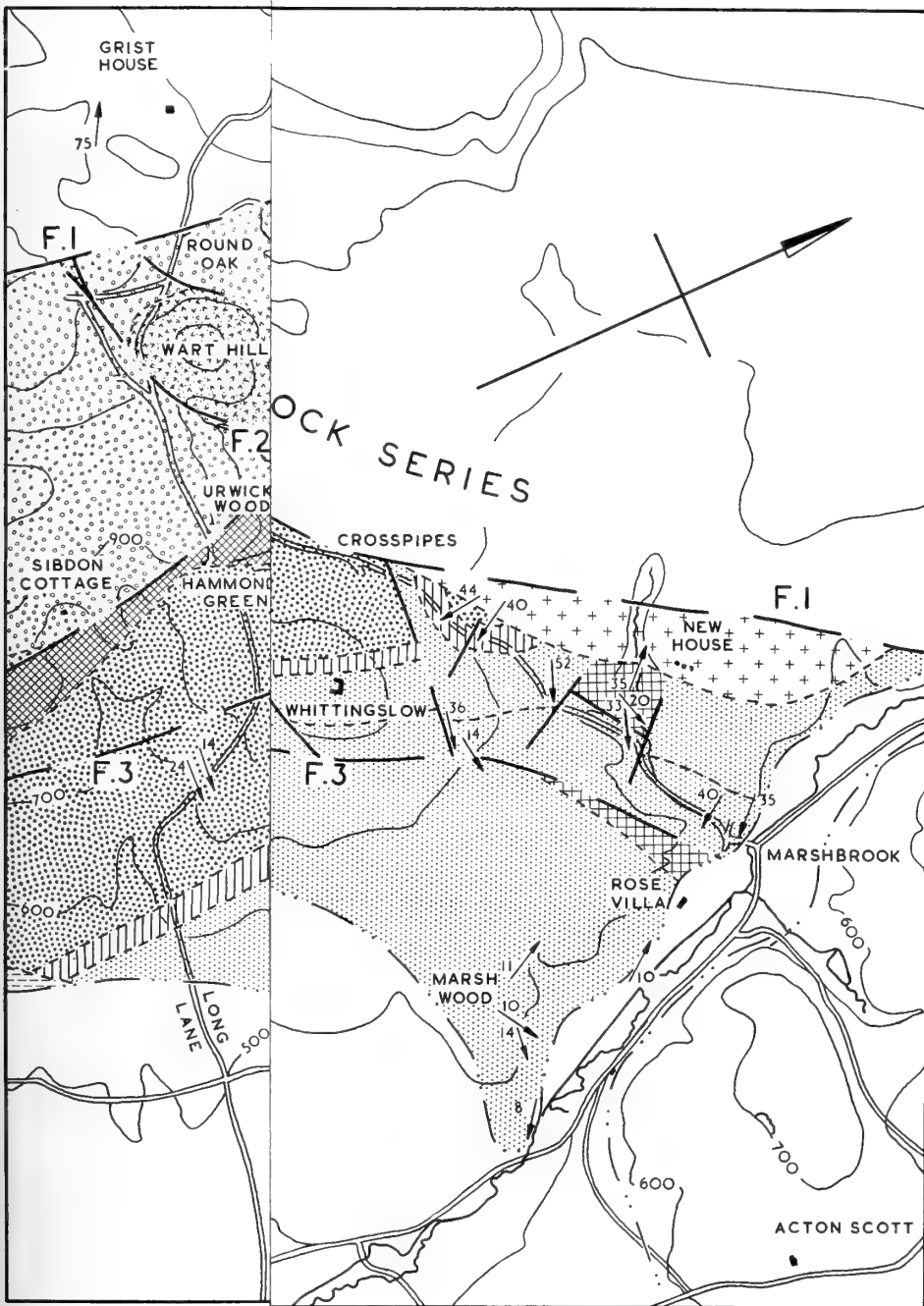
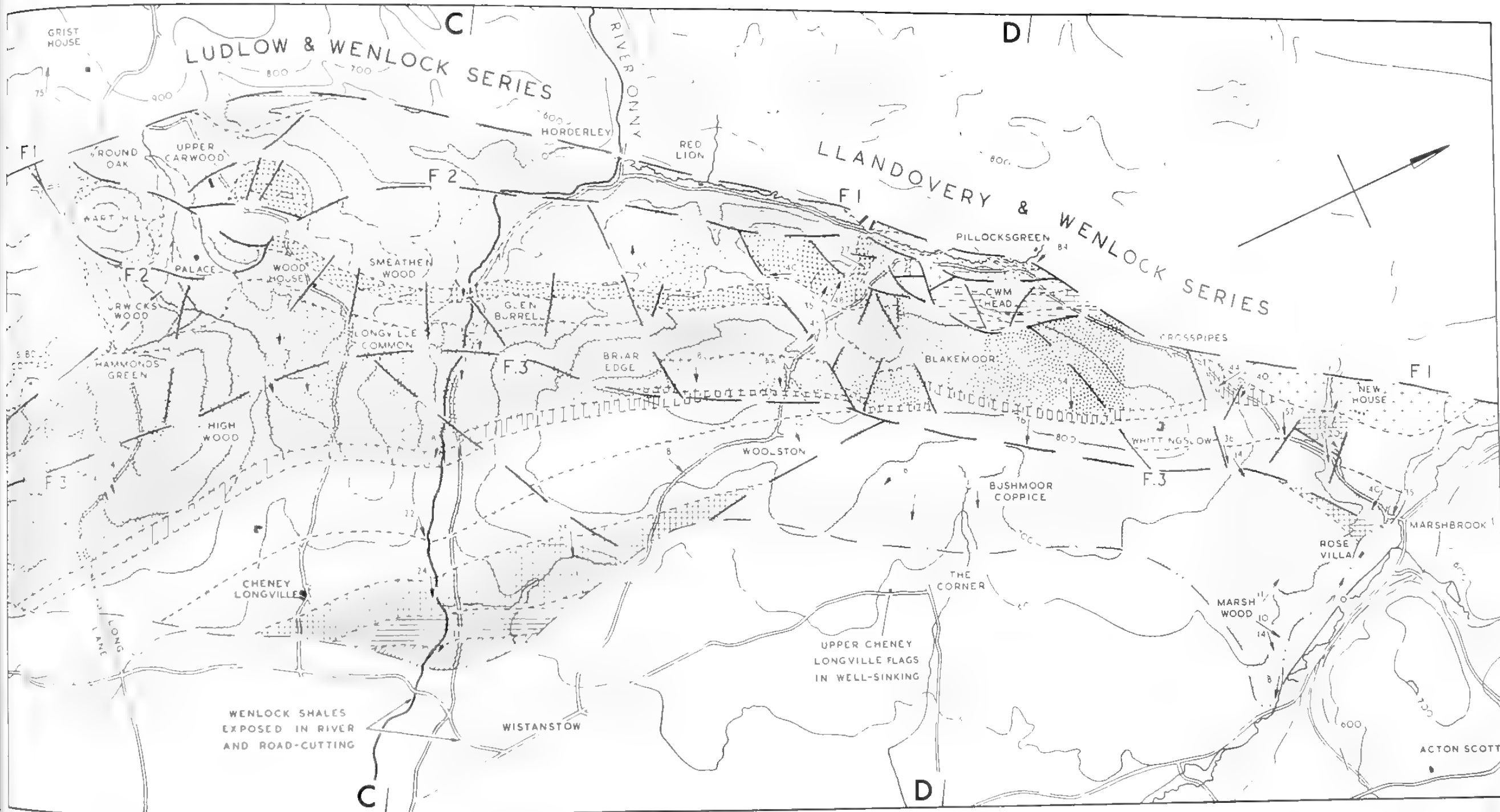


PLATE I





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